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ON THE USE OF THE SUCKING-FISH FOR CATCHING FISH AND TURTLES: STUDIES IN ECHENEIS OR REMORA, II.

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THE FISHERMAN-FISH IN MOZAMBIQUE WATERS

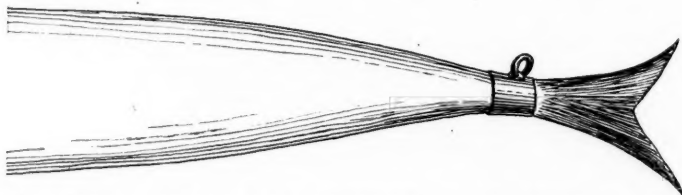
IN the year 1884, Mr. Frederick Holmwood, British Consul at Zanzibar, by publishing an article in the *Proceedings of the Zoological Society of London*, brought this extraordinary use of this remarkable fish to the attention of the scientific world. Chancing on this article, I became greatly interested in the matter and have been led to collect all the available data and to present it herein to those who may be interested.

On a trip in a steam launch from Pemba to Zanzibar, Holmwood had his attention called to a number of remoras which were attached to the sides and bottom of the boat. To these the natives on board gave the name "Chazo." Later at Zanzibar he saw natives digging out diminutive canoes, too small for any normal use, which he was told were for the "Chaza" (so he understood the native word). Now "Chaza" is the word for oysters or other bivalves, hence he thought that these were used to gather such in, but his servant told him that it was a "house" for the "Chazo" or sucking-fish kept by most fishermen in their huts. Later he learned that the native fishermen use the Chazo fish to catch turtles and large fish of any kind. And later still in

Madagascar he was informed that sharks and even large crocodiles were caught by the use of a fish called *Tarundu*¹ which was trained for the purpose. Unfortunately, just here Holmwood gave vent to his incredulity and his informants being greatly incensed refused to talk with him further on this matter.

Holmwood spent considerable time in gaining the confidence of the native fishermen of Zanzibar and was rewarded by being allowed to visit their huts and examine the "Chazo." These he found to be remoras (echeneis?) from 2 to 4.5 feet long and from 2 to 8 pounds in weight. They were kept in the little canoes in the cabins and were so tame as readily to come to the surface of the water at the appearance of their masters, by whom they allowed themselves to be freely handled.

Each Chazo had a strong iron ring or loop fixed just above the tail [text-figure 1] for the purpose of attaching a line to when being em-



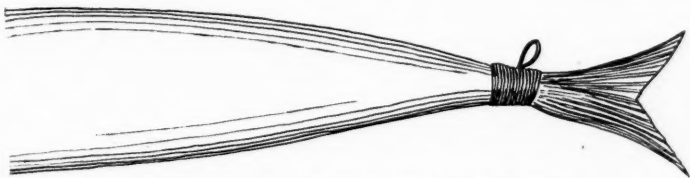
TEXT-FIGURE 1. Tail of sucker-fish with band and ring. (After Holmwood, 1884.)

ployed in hunting. In some cases these appendages had evidently remained on for years, during which the fish had so grown that the iron had become imbedded in a thick fleshy formation. In two instances the ring had been inserted in the muscular substance at the root of the tail [fin], but generally a simple iron band was welded around the thinnest part of the body a few inches from the tail, which kept it from slipping off. To this was riveted a small movable ring or loop resembling that of a watch-handle. In one case [text-figure 2] this loop was fastened on by servings of brass wire in a similar manner to the rings of a fishing rod.

¹ Every effort has been made to trace down the use of the *Tarundu*, but books on the fishes of Madagascar are few, and none of them nor the works of travel consulted have given any clue.

Holmwood purchased one of these fish to send to England but it was killed by a crane. A second one died, probably from lack of a fresh supply of water. He afterwards arranged to buy another on its return from a fishing trip.

It was brought to me a few weeks later minus its ring, and with a large wound or rent above the tail, part of which was gone. The owner declared that it had caught two turtles, which he showed me lying in his canoe, and that it had afterwards affixed itself to a large shark and, holding on after all the spare line had been paid out, the tail had given



TEXT-FIGURE 2. Tail of sucker-fish with loop and servings.
(After Holmwood, 1884.)

way. He stated that the Chazo had then relinquished its hold and returned in its mutilated state to the boat. He assured me that this was not an unusual occurrence and that after a time a fresh ring would be attached and the fish become as useful as before. I endeavored to preserve one of these Chazos in spirits of wine, but failed owing to the inferior quality of the spirit. This specimen measured 2 feet 8 inches in length and weighed $3\frac{1}{2}$ pounds. The sucker contained 23 pairs of lamellæ.

Holmwood wanted to go out with the fishermen and see the fishes at work. But as the distance to the fishing-grounds was considerable, as the trips lasted fifteen days, and as the boats were small and lacked accommodations for a European, he was forced to desist. Thus he failed to become an eye witness to this remarkable procedure.²

² Under date of 1883, a writer signing himself Phil. Robinson published a pamphlet entitled "Fishes of Fancy—Their Place in Myth, Fable, Fairy Tale, and Folk-Lore." This was issued as a hand book for the great International Fisheries Exhibit of that year in London. In this is a verbatim quotation from an article by Holmwood on the use of the fisherman fish in the official catalogue of the exhibition. After much difficulty this official catalogue was located and in it was found Holmwood's original

Holmwood's interesting account is however not the first for the use of the living fish-hook in Mozambique waters. In the year 1829 Lacépède published his "Histoire Naturelle des Poissons," in which, with reference to foreign fishes, he largely made use of the manuscripts of the lamented naturalist, Commerson. On page 490 of Tome III we read:

Commerson . . . has written that this fish (*Echeneis naucrates*) frequents very often the coast of Mozambique, and that near to this coast it is employed for fishing for marine turtles in a very remarkable manner, due to the power which the *Echeneis* possesses of sticking to them. We think that we ought to report here the data which Commerson has collected on this subject so very curious, the only of the kind which has ever been observed. [?]

There is attached to the tail of the living *Naucrates* a ring of diameter sufficiently large not to incommode the fish, and small enough to be retained by the caudal fin. A very long cord is attached to this ring. When the *Echeneis* has been thus prepared, it is placed in a vessel full of salt water, which is renewed very often, and then the fishermen place this in their boats. They then sail towards those regions frequented by marine turtles. These animals have the habit of sleeping at the surface of the water on which they float, and their sleep is so light that the least noise of an approaching fishing-boat is sufficient to wake them and cause them to flee to great distances or to plunge to great depths. But behold the snare which they set from afar for the first turtle which they perceive asleep. They put into the sea the *Naucrates* furnished with its long cord. The animal, delivered in part from its captivity, seeks to escape by swimming in all directions. There is paid out to it a length of cord equal to the distance which separates the sea turtle from the boat of the fishermen. The *Naucrates* retained by the line, makes at first new efforts to get away from the hand which masters it. Soon, however, perceiving that its efforts are in vain, and that it cannot free itself, it travels around the circle of which its cord is some fashion a radius, in order to meet with some point of adhesion and consequently to find rest. It finds this asylum under the plastron of the floating turtle, to which it attaches itself easily by means of its buckler, and

account. He wrote up for this an account of the fisheries of Zanzibar and concluded by giving a short description of fishing with the "chazo." This gives in very abbreviated form the data included above, and ends with the sentence "I hope to forward a specimen of this interesting fish before the close of the exhibition." However, as indicated previously he was unable to do this.

gives thus to the fisherman, to whom it serves as a fulcrum, the means of drawing to them the turtle by pulling in the cord.³

This account of Commerson-Lacépède's is very circumstantial and exceedingly interesting, but it is not the first account of the fisherman fish, and not even the first for East African waters, for in 1809 and 1810 Henry Salt under orders of the British government made a voyage to Abyssinia by way of the Cape and the Mozambique Channel, stopping at Masuril, a village on the harbor of Mozambique. Of this visit he says under date of September 9, 1809 (his book was published in 1814):

As he [the Bishop of Masuril] was aware of my wish to collect the rarities of the place, he made me a present . . . of a large sucking-fish (*Echeneis naucrates*) . . . which had just been brought in by a fisherman. All the Portuguese gentlemen, whom I conversed with on the subject, agreed in assuring me that fish of this kind were employed on the coast in catching turtles. The mode of doing this is by confining the fish with a line to the boat, when it is said invariably to dart forwards, and to attach itself by its sucker to the lower shell of the first turtle found in the water, which prevents its sinking, and enables the fisherman to secure his prey. The reason for the fish fastening on to the turtle is supposed to be done (as the Bishop observed) with a view to self-preservation, and its strength is so great that, when once fastened, the turtle is rarely known to escape.

Earlier still (in the latter half of the eighteenth century) a Swede named Andrew Sparrman made a voyage to the Cape of Good Hope, and in that part of his book dealing with the land of Natal, in the French translation published at Paris in 1787 he wrote:

They [the inhabitants of the country] carry on a very singular method of fishing for turtles. They take alive a fish called Remora, and fixing two cords, one to its head and the other to its tail, they then throw it into the depths of the sea in the region where they judge that there ought to be turtles, and when they perceive that the animal has attached itself to a turtle, which it soon does, they draw in to them the Remora and with it the turtle. It is said that this manner of fishing is also carried on in Madagasear.

³ The same account in brief form is found on pages 170-171 of Pasfield Oliver's life of Commerson (1909).

This account is not found in the English translation of Sparrman's voyage, and I have not had access to the original Swedish edition, but it is found in the French edition in a sort of appendix to that section describing South Africa and is credited to Middleton's "Geography." Inspection of volume I (1777) of this latter work revealed the account substantially as given above, but *in quotation marks* with no hint whatever of its ultimate source.

Humboldt (1826) refers to a similar incident related by Captains Dampier and Rogers. Dampier was worked through twice without finding the reference, but a third going through his "Voyages" page by page revealed it as an annex to part 3 of his volume III, "A Discourse of Winds," etc. (6th edition, 1729). Middleton has copied it almost word for word, so it need not be repeated here. It will be of interest, however, to note that Dampier says that this "annexed paper" was "received from my ingenious Friend, Capt. Rogers, who is lately gone to that place ('Natal in Africk'): and hath been there several times before."⁴

It must be remembered that Holmwood wrote of a fish called *Tarundu* used in Madagascar as a living fish hook, and Lacépède quotes Commerson that a sucking fish is so used in the Isle of France as well as in the Mozambique country and lastly that Dampier quotes Rogers as to this use also in Madagascar. Acting on these hints a good deal of time has been spent in hunting for such accounts not only in books on the fishes of these islands but also in books of travel and at this writing three corroboratory accounts have been found. The first is to be found in Pollen's work on the fisheries of Madagascar (1874).

⁴ The index to Rogers' book ("A Cruising Voyage around the World," 1726) does not contain the words *echeneis*, *remora* or *sucking-fish*. Careful examination of the book, and a minute inspection of that part relating to South Africa, gave no results whatever. Dampier's "Voyages" show that he was keenly observant of natural history objects wherever he went, while Rogers paid little or no attention to such matters. It seems likely that the foregoing account was communicated to Dampier by word of mouth or by letter from Rogers.

For Malagassy waters he quotes the use of *Echeneis* as given by Middleton, Commerson-Lacépède and Salt, and for other waters other authors to be referred to later. He is not clear as to its use in his own time but he seems to indicate that in his day it was so used.

Our next reference is dated 1897. In the *Antananarivo Annual* for that date (published by the London Missionary Society at the capital of Madagascar) there is under "Natural History Notes" a translation by James Wills of a native manuscript which reads as follows:

In the sea off the northwest coast of Madagascar a fish is found called by the people Hamby. It is round and long, somewhat like a lizard, but its tail unfolds for swimming like that of a gold-fish, and it has fins on each side. The length of a full-sized one is about that of a man's arm, and its girth about that of his thigh. Its back fin, from about one quarter of its length up to its head, is just like a brush, and it has a liquid about it, sticky like gum, and when it fastens onto a fish from below with this brush on its head the fish cannot get away, but is held fast. On account of this peculiarity of the *Hamby*, the people of Sambirano use it to fish with. When they catch one they confine it in a cage of light wood, which they fasten in the sea, and feed the fish daily with cooked rice, or cassava, or small fish; and when they want to use it, they tie a long string round its tail and let it go, following it in a canoe. When it fastens on a fish they pull it in and secure the spoil. There is a sea-turtle called by the people *Fanóhana*,⁵ which the *Hamby* is fond of catching, and this the people prize on account of the shell, which is of commercial value.

The above account is given almost word for word by James Sibree in his book "A Naturalist in Madagascar," 1915. Sibree, whose experiences in Madagascar cover a period of fifty years, and who as his book shows was a very close observer, evidently believed in this use of the fish.

THE HUNTING-FISH OF THE WEST INDIES

However, the accounts quoted of the remarkable use of the Remora as a hunting fish in the Mozambique country are not the first that we have of such employment. For the very beginning we must go back to the second

⁵ This is probably the tortoise-shell turtle.

voyage of Columbus to the New World in 1494. This account given below is to be found in the writings of Peter Martyr d'Anghera, who was a prominent figure at the court of Ferdinand and Isabella and the foremost letter writer of his day. In 1511 Martyr published at Seville nine books and part of the tenth of his *Decade I*, the *Decade of the Ocean*, one of the component parts of his "*De Orbe Novo*," which has since appeared in many editions and translations. Possibly the best translation available for the general reader is MacNutt's, published by Putnam in 1912, but as better preserving the spirit of the times, I prefer to give Richard Eden's translation made in 1555, the quaint English of which reads as follows:

At the Ides of Maye, the watche men lokinge owte of the toppe castell of the shyppe towarde the Southe, sawe a multitude of Ilandes standinge thiek together, beyng all well replenished with trees, grasse, and herbes, and wel inhabited. In the shore of the continent, he [Columbus] chaunced into a nauigable ryver whose water was soo hotte, that no man myght endure to abyde his hande therein any tyme. The daye followinge, espyng a farre off a canoa of fyshermen of th(e) inhabitants, fearinge least they shulde flye at the syght of owre men, he commaunded certyne to assaile them pryuiely with the shyppe boates. But they fearinge nothinge, taryed the comminge of owre men. Nowe shal you heare a newe kind of fyshinge. Lyke as we with greyhoundes doo hunt hares, in the playne fieldes so doo they as it were with a huntynge fysshe, take other fysshes. This fysshe was of shape or fourme vnknowne vnto vs: but the body thereof, not muche vnylike a greate yele: havinge on the hynder parte of the heade, a very towgh skynne, lyke vnto a greate bagge or purse. This fysshe is tyed by the syde of the boate with a corde litte downe soo farre into the water, that the fysshe maye lye close hyd by the keele or bottom of the same, for shee may in no case abyde the sight of the ayer. Thus when they espie any greate fysshe, or tortoyse (whereof there is great abundance bygger then great targettes) they let the corde at lengthe. But when shee feeleth her selfe loosed, she enuadeth the fysshe or tortoyse as swiftly as an arrowe. And where she hath once fastened her howld she easteth the purse of skynne whereof we spoke before; And by drawyng the same togyther, so graspeleth her pray, that no mans strength is sufficient to vnloose the same, excepte by lytle and lytle drawinge the lyne, shee bee lyfted sumwhat above the brymme of the water. For then, as sone as she seeth the brightness of the ayer, she lettethe goo

her howlde. The praye therefore, beinge nowe drawn nere to the brymme of the water, there leapeth soodenly owte of the boate into the sea soo manye fysshers, as maye suffice to holde faste the praye, vntyll the reste of the company haue taken it into the boate. Which thinge doone, they loose so muche of the cord, that the hunting fysshe, may ageyne returne to her place within the water: where by an other corde, they let downe to her a piece of the praye, as we use to rewarde greyhoundes after they have kylled theyr game. This fysshe, they caule *Guaicanum*, but owre men caule it *Reuersum*. They gave owre men foure tortoysses taken by this meanes: And those of such hyggenes that they almoste fylled theyr fysshinge boate. For these fysshes are esteemed amonge them for delicate meate. Owre men recompensed them ageyne with other rewardes, and soo let them departe.⁶

Curiously enough a repetition of this story by Martyr himself has been completely overlooked by all who have had occasion to refer to his *Reuersus* story. I myself did not find it until, some two years after making notes and copying his account as quoted above from Eden, I chanced to go over the "Decades" again page by page and stumbled on it. Since Martyr himself has not been quoted directly it will be of interest to give this second account from MacNutt's excellent translation of Decade VIII, Book 8, pages 299-300.

Let us now consider the hunting fish. This fish formerly vexed me somewhat. In my first Decades, addressed to Cardinal Aseanio, I stated amongst other marvels, if I remember properly, that the natives had a fish which was trained to hunt other fish just as we use quadrupeds for hunting other quadrupeds, or birds for hunting other birds. So are the natives accustomed to catch fish by means of other fish. Many people, given to detraction, ridiculed me at Rome in the time of Pope Leo for citing this and other facts. It was only when Giovanni Rufo di Forli, Arehbishop of Cosenza, who was informed of all I wrote, returned to Rome after fourteen years' absence as legate of Popes Julius and Leo in Spain, stopped the mouths of many mockers, and restored me my reputation for veracity. In the beginning I also could hardly believe the story, but I received my information from trustworthy men whom I have elsewhere cited, and later from many others.

Everybody has assured me that they have seen fishermen use this fish just as commonly as we chase hares with French dogs, or pursue the wild deer with Molossians. They say that this fish makes good eating.

⁶ This is a literal copy of Arber's literal copy of Eden, save that the old-fashioned f-shaped s has had to be replaced by the modern letter.

It is shaped like an eel, and is no larger. It attacks fish larger than itself, or turtles larger than a shield; it resembles a weasel seizing a pigeon or still larger animal by its throat, and never leaving go until it is dead. Fishermen tie this fish to the side of their barque, holding it with a slender cord. The fish lies at the bottom of the barque, for it must not be exposed to the bright sun, from which it shrinks.

The most extraordinary thing is that it has at the back of its head a sort of very tough pocket. As soon as the fisherman sees any fish swimming near the barque, he gives the signal for attack and lets go the little cord. Like a dog freed from its leash, the fish descends on its prey and turning its head throws the skin pouch over the neck of the victim, if it is a large fish. On the contrary, if it is a turtle, the fish attaches itself to the place where the turtle protrudes from its shell, and never lets go till the fisherman pulls it with the little cord to the side of the barque. If a large fish has been caught (and the fishermen do not trouble about the small ones), the fishermen fasten stout cords to it and pull it into the air, and at that moment the hunting-fish lets go of its prey. If, on the contrary, a turtle has been caught, the fishermen spring into the sea and raise the animal on their shoulders to within reach of their companions. When the prey is in the barque, the hunting-fish returns to its place and never moves, save when they give it a piece of the animal, just as one gives a bit of quail to a falcon: or until they turn it loose after another fish. I have elsewhere spoken at length concerning the method of training it.⁷ The Spaniards call this fish *Reverso*, meaning one who turns round, because it is when turning that it attacks and seizes the prey with its pocket-shaped skin.

This remarkable story of Martyr's has been repeated by many writers from his day almost to this and especially by the Spanish chroniclers of the early political and natural history of the West Indies. Many of these, however, add to the original story certain details which will be of interest to include herein.

The first of these is the historian Oviedo, whose "*Sumario*" was published but five years (1516) after Martyr's "*Decades of the Ocean*," and whose "*Chronicles*" were first published in 1535. My excerpt is taken from the Salamanca edition of 1547, but there is no reason to think that this particular account differs from that found in the earlier editions. We will let Oviedo

⁷ This account does not seem to have been preserved. At any rate it is not to be found in MacNutt's translation.

speak for himself, and his account is all the more interesting and valuable because he gives certain details as to the training and care of the fisherman fish which are absent from the other accounts, and of which he seems possibly to have had some personal knowledge.

There is a fishing of these Manati and of the tortoise in the islands of Jamaica and Cuba, which, if what I shall now say were not so public and well known, and if I had not heard it from persons of great reliability, I should not dare to write. And also it is believed that when there were many Indians, natives, on the island Espagnola, they also caught these animals with the Reversus fish. And since the discussion of the history has brought me to speak of the animal, the Manati, it is better that it is to be known that there are some fish as long or longer than a *palma*, which they call the Reversus fish, ugly in appearance but of great spirit and intelligence, which sometimes happens to be caught in their nets along with other fish. This is a great fish and among the best in the sea for eating, because it is dry and firm and without watery parts, or at least it has very few; and many times I have eaten of it and so am able to testify of it.

When the Indians wish to tame and keep any of these Reversus fishes for their use in fishing, they catch it small and keep it always in salt water from the sea, and there they give it food and make it tame, until it is of the size which I have said or a little more, and fit for their fishing. Then they take it out to sea in the canoe or boat, and keep it there in salt water and fasten to it a cord delicate but strong. Then when there is seen a tortoise or any of the large fish which abound in these seas, or some of these Manati or whatever it may be that happens to go on the surface of the water in such a way as to attract attention, the Indian takes this Reversus fish in his hand and strokes it with the other, and tells it to be *manicato*, which means strong and of good courage and to be diligent, and other words exhorting it to bravery, and to see to it that it dare to grapple with the largest and best fish that it may find there [where the fishing is to take place]. And when the Indian sees that the best time has arrived, he lets it go and even throws it in the direction of the large fish. Then the Reversus goes like an arrow and fastens itself on the side of a turtle, or on the belly, or wherever it can, and thus clings to it or to some other large fish. This one, when it feels itself seized by the little Reversus, flees through the sea in one direction or another; and in the meantime the Indian fisherman lengthens the cord to its full length, which is many fathoms, and at the end of this is fastened a stick or cork that it may be for a signal or buoy which will remain on top of the water. In a little while the Manati or turtle, to which the Reversus has attached itself comes to the

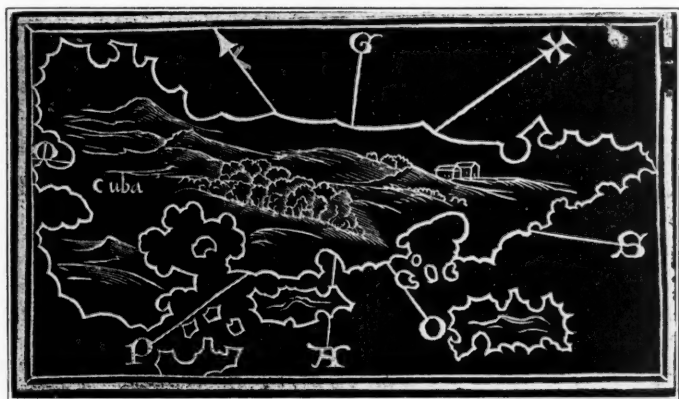
shore, and then the Indian fisherman begins to draw the cord into his canoe or boat and when there are but a few fathoms left, he commences to draw it in carefully and slowly, guiding the Reverso and the prisoner to which it is attached until they reach land and the waves of the sea throw them out. The Indians who are engaged in the fishing leap out on land and if the prisoner is a tortoise they turn it over even before it has touched the ground and place it high and dry because they are great swimmers; and if it is a manati they harpoon, wound and kill it. When the fish has been taken to the land it is necessary very carefully and slowly to release the Reverso which the Indians accomplish with soft words, giving it many thanks for what it has effected, and thus they release it from the other large fish which it captured and to which it is so strongly attached that if it were forcibly removed it would be broken to pieces; and thus in the manner I have described are taken these large fish for whose chase and capture it seems that nature has made the Reverso the sheriff and executioner. It has some scales similar to the corrugations [*grades*] such as are found in the palate or upper jaw of man or horse and therewith certain spines very thin, rough and strong, whereby it attaches itself to the fish it seeks. And the Reverso has these scales or corrugations full of these spines over the greater part of the outer body, especially from the head to the middle of the body along the back and not on the belly, but from the middle of the body up; and from this circumstance they call it the Reverso because with its shoulders it seizes, and fixes itself to fishes.

So credulous is this generation of those Indians that they believe the Reverso well understands human speech and all those words of encouragement the Indian says before releasing it for an attack on the tortoise, manati or other fish, and that it understands also the thanks they afterward give it for what it has done. This ignorance arises from a failure to comprehend that this is a natural characteristic, because it happens many times in the great ocean as I have frequently witnessed, that when a shark or tortoise is captured, Reversos, without having been directed, are found attached to these fish and are broken to pieces on detaching them. From which we may infer that it is not in their power to release themselves after they have attached themselves except after an interval of time or from some other cause I have not determined; because one must think that when the shark or tortoise is taken the Reversos attached thereto would flee if they could. The fact is, as I have said above, for each animal there is its constable.

In 1527, Benedetto Bordoni published his "Isolario." In it is a brief account of the fishing in that locality called Queen's Gardens. It seems to be an abbreviated transcript from Peter Martyr and adds nothing new, save a

map of Cuba, showing the islands off the southern coast among some of which the fishing with the Guiaean was observed. This seems to be of enough interest to be reproduced herein as text-figure 3.

In 1553, Gomara published at Medina del Campo his "Historia General de las Indias." On folio XIII is found an abbreviated copy of Oviedo's account of the Reversus fish, but as it contains nothing new it need not detain us.



TEXT-FIGURE 3. The Island of Cuba with the Jardinelas de la Reina to the south. (After Bordonl, 1527.)

The greatest of the encyclopedic writers on natural history in the Renaissance times was the Swiss, Konrad Gesner, who was too good a searcher for the marvellous to let such a story as this escape him. His account (1558) is a somewhat abridged but yet almost literal translation of Peter Martyr. However, he gives us a figure of a hunting scene, showing how this fisherman-fish was used, and this is reproduced herein as Fig. 4, Plate I. The Reversus fish is shaped like an eel and has a great bag or pouch attached on the back of its neck. This pouch has just been thrown over the head of what appears to be a seal (probably meant for a manatee), while a turtle looks on in amazement from one side. In the background in this

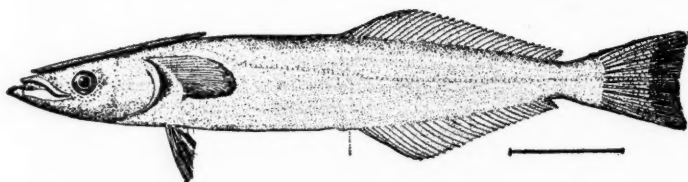
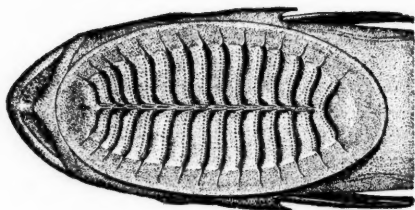


Figura haec desumpta est ex tabula quadam descriptionis orbis terrarum.



PLATE I

- FIG. 1. Sucking-disk of Remora. After Jordan and Evermann, 1906.
 FIG. 2. *Leptechencis naucrates*. After Jordan and Evermann.
 FIG. 3. *Remora brachyptera*. After Jordan and Evermann.
 FIG. 4. The first known figure of fishing with the fisherman fish. After Gesner, 1558.

boat are the fishermen, one of whom holds one end of a line the other end of which is tied around the anterior part of the body of the eel-like fish.⁸ In a sort of post-script Gesner refers to another hunting-fish which is similar to but smaller than the above. This reference, however, is not clear.

The first user of the name *Guiacan* for our fish was Peter Martyr; other and later writers take the name from him. Considerable effort was made to run down this word and to ascertain its meaning. It was finally found in Bachiller y Morales's "*Cuba Primitiva*" (1883). Here we are told that

Guiacan was the name the Indians gave to the fish which the Spaniards called *Reverso*, and which served them in fishing; because tied by the tail, they fixed themselves to the tortoise and other prey which they did not release, rendering thus a useful service.

Earlier than Bachiller y Morales, another writer, Raymond Breton (1665), calls the huntsmen fish "*Iliouali*" and says that it is a fish which has on its head a membranous plaque, and if it attaches itself to the canoe it can with difficulty be removed save by breaking it into fragments.

That part of Gesner's "*Natural History of Animals*" which has to do with fishes was worked over in German and published in 1575 as "*Das Fischbuch*." In it on page L is found the figure of the hunting scene just referred to and an abbreviated account of the use of the fish as a living fish-hook. Here also there is an account of

⁸ Every effort has been made to ascertain the original of this figure. Presumably it is from an insert in some contemporary map or similar publication. Dr. Eastman personally made a search through the rich collection of Americana in the New York Public Library, the able curator of which, Mr. V. G. Paltsits, had to confess himself at a loss. I myself have worked through the collection of reproductions of old maps in the same library but in vain. Finally the question was submitted to Mr. E. A. Reeves, the learned curator of maps of the Royal Geographical Society, London, who courteously made a lengthy search through all the old maps under his care. Finding nothing he passed the question along to the authorities of the British Museum, who in turn could give no help. So the origin of this interesting and oldest figure still remains a mystery.

another *Reversus*. Apparently herein Gesner has mixed certain data from Oviedo with the legends of another *Reversus* covered with sharp spines.

It seems that in the writings of these old Spanish historians two fishes are described called *Reversus*;⁹ one the anguilliform kind, having a pouch or sucker on its head, evidently a *Remora*, or, since it grows larger, an *Eche-neis*; the other the squamous kind covered with scales bearing long spines, evidently the swell fish, *Diodon*. Concerning these fishes Dr. C. R. Eastman has written several interesting and valuable papers to which the attention of the reader is called. (See Bibliography, Eastman 1915, 1915a, 1916.)

We next hear of the *Reversus* in the writings of one Antonio Galvano. His book, "The Discoveries of the World from their first Original unto the Yeare of our Lord 1555," was published in the original Portuguese in 1563 under the editorship of his friend, F. Y. Sousa Tavares, and translated and reprinted at London in 1601 by Richard Hakluyt. Neither of these editions being available. I have had to content myself with the Hakluyt Society's reprint¹⁰ found in Vol. 30, 1862, as edited by C. R. D. Bethune. Here there is a short paragraph in which the use of the anguilliform eel is attributed to the squamous form. Nothing new is added and no quotation will be given.

⁹ The *reversus* or "upside down" fish was undoubtedly so named because when attached to the carapace of a turtle its belly was turned upward or outward, as also when it was attached to the side of a fish—in any case its natural position was reversed. *Diodon* when it inflates its belly with air floats at the surface belly up, hence it too was a *Reversus* fish.

¹⁰ It is interesting to note that in the Hakluyt reprint the *Reverso* story is put in square brackets. This considerably confused me and lest others be similarly thrown off the track it seems well to add this note from Mr. C. K. Jones of the Library of Congress, "Hakluyt, when publishing his 1601 edition was unable to find the original. The Hakluyt Society in preparing its 1862 edition secured a copy of the original publication of 1563 from John Carter Brown; and from this copy the Portuguese text was printed." It seems that Hakluyt included in his 1601 edition the *Reverso* story from original histories. However, in the original Portuguese text, Mr. Jones finds the *Reverso* story without brackets.

We next hear of the fisherman-fish in Herrera's "*Historia Generale de las Indias Occidentales*" published in 1601. In Capt. John Stevens's translation we read:

They [the Indians] fished on, and took some fishes they called *reves*,¹¹ the biggest of them about the size of a Pilehard, having a roughness on the belly [?], with which they cling so fast, wheresoever they first take hold, that they must be torn in pieces before they can be torn off again. They ty'd these by the Tail with a small Thread, about two hundred Fathoms more or less in Length, and the Fish swimming away on the Surface of the Water, or but a little under it, when it came to where the Tortoise was in the Water, it clung to the under Shell thereof, and then the Indians drawing the thread, took a Tortoise that would weigh a hundred Weight, or upwards. After the same manner they took Sharks, which are most cruel bloody Fishes that devour Men.

Next comes Ramusio, whose "*Della Historia dell' Indie*" bears date Venetia, 1606. This appears to be merely a translation into Italian of Oviedo's Spanish work. At any rate it adds nothing to our knowledge of the hunting-fish, and may be passed over with this brief notice.

Another of the "fathers" of ichthyology is Aldrovandi, whose great work was published in 1613. He figures and describes both kinds of the *Reversus*. In general he follows Peter Martyr, but it is very clear that he copies Gesner. However, he has had Gesner's fishing scene redrawn, as may be seen from the reproduction of it herein (Fig. 5, Plate II). The boat and boatman are omitted, as is the cord around the neck of the fish, the seal-like animal has been replaced by another probably intended to represent a manatee, the turtle is entirely different, and lastly the head of the *Reversus* is not at all that of Gesner's figure. This is much larger, the teeth are more marked, the upper jaw has a hooked beak; and the bag of skin comes more distinctly off the top of the head, and is smaller at the base and has more longitudinal striations. And yet for all these changes it is plainly Gesner's figure.

¹¹ *Reves* is of course a variant of the word *Reversus*, an abbreviation possibly.

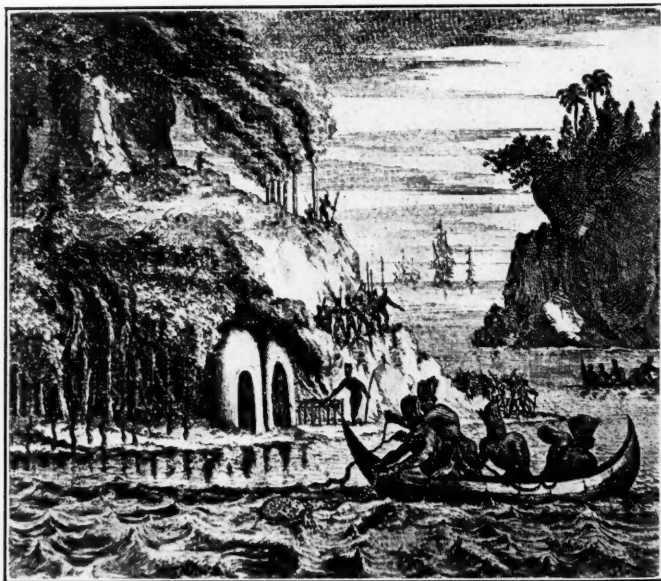
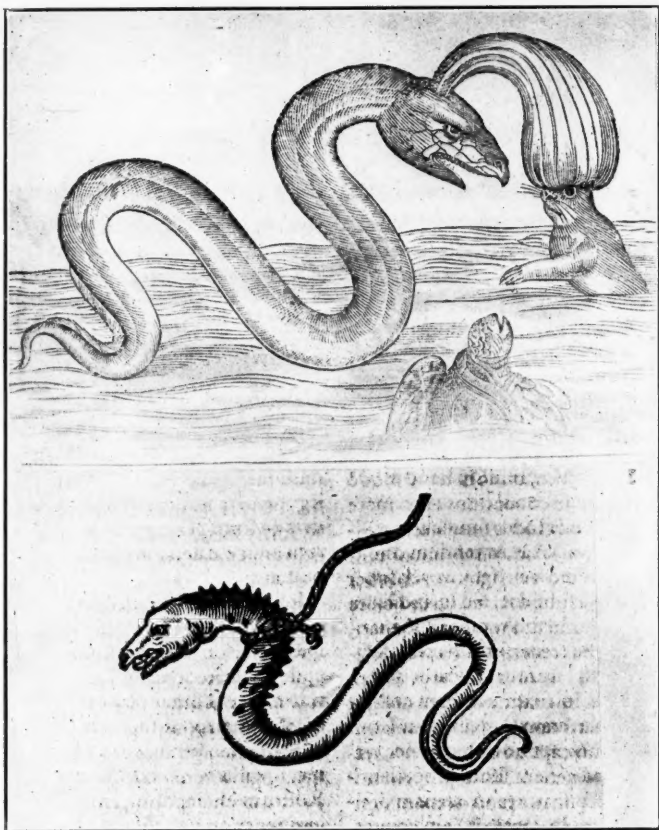


PLATE II

FIG. 5. The Indian anguilliform Reversus. After Aldrovandi, 1613.

FIG. 6. Reversus or Gulacanus, according to Nieremberg, 1635.

FIG. 7. Fishing with the Reversus, from Ogelby's "America," 1671.

In another place Aldrovandi gives a figure of the spinous *Reversus*, but in his account of this form he gets his data badly mixed since much of it is the data which Peter Martyr ascribes to the anguilliform variety. In neither account does Aldrovandi offer anything new.

We now come to a Spanish work published in Mexico City five years before the Pilgrims landed on Plymouth Rock and when Jamestown was but eight years old. This is Hernandez's work (1615) on the nature and virtues of the plants and animals used in the practise of medicine in New Spain. How he brings in the *Remora* is not clear, but he attributes his account to Oviedo, the actions of whose anguilliform *Reversus* he describes in his (Oviedo's) own words. However when he attempts to further describe the fish he gets his account tangled up with that of the porcupine fish. He does not seem to have ever seen either fish.

In 1635, Joannes Eusebius Nieremberg, a Jesuit priest, who was professor of physiology in the Royal Academy of Madrid, published his "*Historia Naturae*" in folio form. This is a compilation of not very great value, the less so because the references are not set forth clearly. Our interest in his book, in which he quotes Peter Martyr, Oviedo, Hernandez and another to be referred to later, is chiefly centered in his figure of the *Reversus* or *Guiaacanus*. This is reproduced here as Fig. 6, Plate II. This is plainly Gesner's figure with the addition of a sort of saw-toothed mane on the anterior dorsal region.

Ogilby, whose huge tome was published in 1671, had evidently never seen the *Guiaean*, but he inserted on page 49 of his "*America*" such a quaint and interesting figure of his conception (or his artist's) of how this fishing was carried on, that this is reproduced herein as Fig. 7, Plate II.

The Dutchman, Th. van Brussel, in 1799 published a very interesting account of the *Reversus*; but a careful translation of his Dutch shows that it is but a translation of Martyr and Oviedo, and further that he confuses the

anguilliform and squamous forms of the *Reversus*—a figure of the latter being given. He also need not detain us.

From this time on a long succession of writers repeat the tale. Thus we find it in Shaw's "Zoology," Vol. IV, 1803; Humboldt's "Essai Politique sur l'Ile de Cuba" (1826), his "Receuil d'Observations de Zoologie et Anatomie Comparée" (1833) and in the "Personal Narrative" (English translation, 1860). We also find it in most if not all of the "Lives" of Columbus, notably Irving's (1828), Winsor's (1892), and last and best Thacher's (1903).

To these foregoing accounts we may add a brief note which may be of interest. Bernabe Cobo was a Spaniard (born 1582, died 1657) who wrote his "*Historia del Nuevo Mundo*" and at his death left it in manuscript where it remained until found, edited and published by the Spanish naturalist, Marcos Jimenez de la Espada, towards the close of the last century. Volume II, Sevilla, 1891, contains Cobo's story which turns out to be the familiar paraphrase of Oviedo's account. Absolutely nothing new is added.

We now come to a consideration of the sources of the various accounts of the use of the sucking fish as a living fish-hook in the West Indies. First of all plainly these later accounts are all echoes of Peter Martyr, or of Oviedo, or of both. Then these further questions naturally arise: Is Peter Martyr's "Decade of the Ocean" in 1511 the first account published? And secondly what is the ultimate source of these earliest accounts? In answering these questions I have had three invaluable sources of information. The one is Justin Winsor's keenly critical life of Christopher Columbus, the second is John Boyd Thacher's monumental work on Columbus (Vol. II, 1903) and the third is the continued advice and unfailing help of my friend, the late Dr. Charles R. East-

man.¹² Dr. Eastman became interested in the subject while working on the great "Bibliography of Fishes" published by the American Museum of Natural History, and finding that I was collecting data for a series of papers on Echeneis most courteously turned over to me invaluable material and aided me in every possible way. At the very time when I was slowly tracing these accounts backward towards their ultimate source, Dr. Eastman in the most brilliant fashion ran these stories down to the original recorder himself.

First of all let us see if Martyr's account in 1511 is the first published account of the interesting phenomenon. To this the answer must be "No!" Dr. Eastman sent me the following extract from "Libretto de Tutta la Navigazione de Re de Spagna et de le Isole et Terreni Novamente Trovati," Venezia, April, 1504 ["A Little Book in Regard to All the Navigation of the King of Spain to the Islands and Newly Discovered Lands"]:

Continuing [along the coast of Cuba] they found further onward fishermen in certain of their boats of wood excavated like *zopoli*, who were fishing. In this manner they had a fish of a form unknown to us, which has the body of an eel, and larger, and upon the head it has a certain very tender skin which appears like a large purse. And this fish they drag, tied with a noose to the edge of the boat, because it cannot endure a breath of air. And when they see any large fish or reptile [*biscia*] they loosen the noose, and this fish at once darts like an arrow at the fish or reptile, throwing over them this skin which he has upon his head; which he holds so firmly that they are not able to escape, and he does not leave them if they are not taken from the water, but as soon as he feels the air he leaves his prey and the fishermen quickly seize it. And in the presence of our people they took four large turtles which they gave our people for a very delicate food.

After Dr. Eastman had sent me the above translation from the Libretto, I very carefully worked over Volume II of John Boyd Thacher's monumental life of Columbus

¹² The recital may perhaps not be devoid of either interest or value if the steps are set forth by which Dr. Eastman and myself, working separately and at a great distance from each other, traced this interesting story back to its original narrator. But it should be said here that Dr. Eastman reached the goal first, and that my efforts were chiefly confined to confirming his results, and clearing up certain details.

and from it much of the data following have been obtained. Only one copy of the Libretto is known in the world, and it is preserved in the San Marco Library at Venice. Thacher traced the original manuscript copy of the Libretto to the ownership of a man named Sneyd, living at Newcastle-on-Tyne, but was refused even the sight of it much less a chance to make photographs. However the authorities of the San Marco Library were men of different caliber, and Thacher reproduces in his book the whole Libretto page by page. And I in turn reproduce here as text-figure 4 a part of Thacher's reproduction of the page giving the Reversus story. It is from chapter XV.

Trouarono dapoi p:u auân al-
cuni pescadori i certe sue barche de uno legno cauo come zopoli ch pe
scauão. In q̃sto mō haueuão un pesce duna forma a noi incognita ch ha
el corpo d' aguilla: & mazor: & supra ala testa ha certa pelle tenerissima
che par una borsa grãde. Et q̃sto lo tieono ligato cō una trezola ala spō
da dela barcha p che el nō po patir uista de aere: & cōe uedēo alchun pe
sce grãde o bisia scudelera li lassāo la trezola: & q̃llo subiro corre como
una fletta al pesce o ala bischia: butādoli adosso q̃lla pelle ch tien sopra la
testa cō laq̃l tie tãto forte ch se ipar nō possono: & non li lassā si noi tiri
for de laq̃: elq̃i sut ito sentiro laire lassā la preda. & li pescadori p̃sto api-
glare. Et i p̃ntia de li ñri p̃fero. iiii. gran calãdre. leq̃e donoronno ali ñri p
cibo dilaucissimo.

TEXT-FIGURE 4. Page from the Libretto, 1504, whereon is contained the first printed account of the fisherman fish. Reproduced from Thacher's "Christopher Columbus," II, 1903.

The Libretto of 1504 was the first collection of voyages to the new world ever printed, and as such is of great interest to scientific men for more reasons than those merely pertaining to this article; hence it may be of interest for us to consider for a few minutes its history, which is as follows.

Peter Martyr, born in Italy, was a courtier and literary man of high standing in the entourage of Ferdinand and Isabella. Thacher says: "Peter Martyr d'Anghera may be said to have composed the matter in this little book, writing it in Latin from a series of letters addressed by

him to various noted persons. These letters were written immediately after the events they describe. They bear the first news. They reflect first impressions. . . . This work was put into its present narrative form some time prior to the summer of 1501."

There now enters upon the scene another Italian letter writer, one Angelo Trivigiano, who was secretary to Domenico Pisani, the Venetian ambassador at the Spanish court. Thacher publishes copies of three letters which Trivigiano wrote in 1501 to the Venetian admiral and historian Domenico Malipiero (whose retainer he seems to have been) transmitting copies of various sections of a "voluminous work" on the voyage of Columbus "composed by an able man." Trivigiano nowhere names Peter Martyr as the author, but in all three of the letters he says that the author is the ambassador of the Spanish court to the Sultan of Egypt, and contemporary history informs us that this was no other than Peter Martyr, who left Granada for Egypt, August 14, 1501.

The contents of the *Libretto*, in Peter Martyr's own words, baring an introductory paragraph by Trivigiano descriptive of the personal appearance of Columbus, was turned over by Malipiero to Albertino Verzelles da Lisona, and by him issued in the Venetian dialect as a printed book on April 10, 1504.¹³

(To be Continued)

¹³ The only other historian of Columbus whom I have found to make mention of the *Libretto* is Winsor, who says that the first seven books of the first Decade were sent in Italian to Venice and there issued as a printed book of 16 leaves in April, 1504.

THE GERM PLASM OF THE OSTRICH

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A

The *germ plasm* is fundamental and remarkably conservative . . . when the germ plasm changes it does so as a result either of wholly internal physiological causes, or of very extraordinary environmental stresses acting directly upon the germ cells . . . mixing of germ plasms, in and of itself, does not mutually alter hereditary determiners . . . selection only acts as a mechanical sorter of existing diversities in the germ plasm and not as a cause of alteration in it.

B

Hereditary determiners or factors fluctuate regularly and frequently, if not indeed usually, and in high correlation with somatic characters . . . mixing of germ plasms in fertilization alters hereditary determiners mutually and hence is, in and of itself, a cause of genetic variations . . . a purely external agent, the continued selection of personal *somatic* qualities, will alter the germ plasm.

IN the above clear, concise phrases, sometimes with supporting amplification, Dr. Raymond Pearl,¹ in the presidential address before the New York Meeting of the American Society of Naturalists, 1916, contrasts the attitude of two sections of American geneticists with regard to the manner of changes in the germ plasm, as affording so much somatic material upon which selection may possibly work in the evolution of animals and plants.

So much evidence is already available for discussion on the merits of the one side or the other that it would appear gratuitous to add more, and one can well appreciate the advice which Pearl gives to get down to *more, and more searching, investigations as to the causes of genetic (factorial) variation*. The case of ostrich breeding in South Africa however affords such direct evidence bearing upon

¹"The Selection Problem," AMERICAN NATURALIST, February, 1917, Vol. 51.

most of the dicta that it is thought an account may be welcomed by geneticists. At any rate it may be added to the already voluminous "Experience of Practical Breeders," containing facts which will need to be reckoned with in any explanation of the actual causes of germinal changes. The ostrich affords an example of an animal only recently domesticated and still in the making, and we have before us the practical methods followed and the results obtained, enabling us to deduce in some measure the genetic principles involved. The endeavor will be to see what contribution its germ plasm has to make to each of the contrasting statements at the head of the paper, not forgetting that we know but little of the nature of the germ plasm and its changes except from their manifestation in the soma. It may be there is truth in both attitudes.

I

"The germ plasm is fundamental and remarkably conservative."

Ostrich farming on methodical lines was first undertaken in South Africa about fifty years ago. The beginnings were made with chicks obtained from wild nests, as unless "tamed" from an early age control of the adults is afterwards impossible. So remunerative did the industry prove to be that with the exception of one or two setbacks it advanced with great rapidity until at its zenith, the year before the war, 1913, nearly 1,000,000 domesticated birds were recorded, yielding an export of 1,023,307 lbs. of feathers at a value of \$15,000,000, forming with gold and diamonds a triad contributing much to the prosperity of South Africa. With the advent and continuance of the war depression of a most severe character set in among ostrich farmers, and the number of birds has been reduced by about two thirds.

In the early days of the industry very little account was taken of the quality of plumage produced, and any bird reaching sexual maturity (three to four years) was employed as a breeder. Within the past two or three decades

however the greatest attention has been devoted to the many characters of the plume and only the best plumage birds have been employed as breeders, the chief reason being the great difference in returns from clippings of high quality compared with those of an ordinary or inferior type. An intensive study has arisen in connection with the various structural details of the feather and also with the measures necessary for their production in the highest state of excellence; among the latter are included both the feeding and management of the birds as well as selection in breeding. It is probably safe to say that no domestic animal has been more intensively and intelligently studied by the farmer than the high grade ostrich, or more pampered in its treatment. Breeding sets, a cock and a hen, known to produce progeny giving superior plumage have frequently realized as much as \$5,000.

The "points" of the ostrich plume relate to details concerning the length, width, density, lustre, shapeliness and evenness of the flue (vanes) and the form and strength of the shaft, and a highly technical terminology has arisen in connection therewith. An ostrich produces annually from 200 to 300 commercial feathers, belonging to a dozen or more different classes—whites, byocks, blacks, drabs, floss, tails—each with its many subdivisions. Each individual feather is handled and specially examined several times in the processes of clipping, arranging, sorting and selling, before being exported, and prior to the war two or three hundred millions of feathers were in this manner passed in review.

Under such keenly discriminating circumstances it will be understood that if any plumage variation presented itself it would be at once recognized and brought to general notice. A bird giving rise to a departure of any moment in a desirable direction in connection with any of the feather points mentioned would represent a fortune to its owner. But not a single case has ever been forthcoming. *Without any hesitancy it can be affirmed that in the course of the fifty years during which the ostrich has*

been domesticated it has never produced a feather variation, germinal in its origin, such as could be regarded as of the nature of a sport or mutation. Feather irregularities and abnormalities are by no means infrequent, but can generally be ascribed to some injury to the feather germ or follicle in the process of quilling, or to malnutrition. Any peculiarity of this nature is usually forwarded to the writer, and some of the more common irregularities have already been described.² They are never hereditary peculiarities.

This stability on the part of the various structural details of the feather has continued despite the great changes to which the ostrich has been subject as a domesticated creature. The birds are fed on the most nourishing and stimulating of foods, the farmer having no option in the matter if he is to secure a feather crop of the highest quality; also they may be transferred from the moist coastal planes to the dry and arid interior at an elevation of 5,000 or 6,000 feet, a change involving great variation in temperature, pressure and other conditions. As an epidermal product, growing at the rapid rate of a quarter of an inch daily, the feather is extremely sensitive to changes in nutrition and climatic conditions, often responding to the small differences in blood-pressure between day and night. Yet all the modifications resulting from these influences are somatic; no hereditary germinal alteration has ever manifested itself.

Like so many other African animals, the giraffe, hippo, rhino, elephant and ant-bear, the ostrich is a survival of ancient days, a left-over, and as becomes a creature of long ancestry is fixed and immutable with regard to the many characteristics of its plumage. Numerous germinal changes have appeared in the past and survive to-day in the various feather types recognized by the specialist, all of which breed true; but it can justly be claimed that no further alteration has taken place during the past fifty

² "Experiments with Ostriches, XXI., Feather Irregularities," *Agric. Journ.*, Union of South Africa, August, 1912.

years, in spite of the many environmental changes to which the bird has been subject. As regards the structural details of the feather the germ plasm of the ostrich fully confirms the statement with which the section opens.

II

"Mixing of germ plasm, in and of itself, does not mutually alter hereditary determiners."

If the plumage characters of the ostrich are so immutable what then is the objective in breeding? The original wild stocks with which the farmer commenced in the sixties differed much among themselves in the structural minutiae of the feather, and the most desirable of the various feather points were distributed among many strains. *The earnest endeavor of the ostrich breeder is to combine in the single plume the best of all the many desirable features originally scattered throughout the wild birds.* The ultimate purpose of every breeder is the same—to produce a plume combining the maxima of all the available feather characters; a plume having the greatest length, width, density and luster and the most perfect shape, supported on a round, strong, slender shaft. On the original birds the largest plumes had for the most part a coarse, loose, unshapely flue, while the most compact, shapely, lustrous, graceful plumes were generally small. The whole effort is to combine the maximum size with all the so-called "quality points"; no other feature of the bird is taken into account in breeding, as none has any commercial value or is known to be in any way correlated with feather production. The problem appears simple, though it is taking years to accomplish; progress is being made each year, but the ideally perfect ostrich plume is not yet.

The genetical methods of the farmer are likewise simple. He proceeds entirely in the belief of a blending inheritance, which though doubtful in theory is succeeding in practise. He starts with a bird which produces plumes the most nearly approaching his ideal, and mates

it with another most closely resembling it, but perhaps lacking or surpassing in one or more points; another season he may resort to a different mating to secure other features. From different breeding sets he may rear two or three hundred chicks in a season. The progeny being mostly intermediates and showing much variation he selects when mature the most desirable among them as breeders, or maybe, being weak in some particular point, he will purchase or exchange with another breeder in whose birds the character is strong. By this method, essentially one of hybridization, the ideal plume is being slowly built up. Sometimes by a fortunate mating one breeder will be ahead and sometimes another, a successful competitor at a Feather Show being inundated with orders for breeding birds and chicks and his fortune well assured. Despite the variability in the progeny no breeder can afford to "fix" his strain by a measure of inbreeding, lest while doing this another may get ahead. Taking all the economic and biological circumstances into account the geneticist has little he can contribute to such a practical effort; he can but assist by endeavoring to deduce and explain the principles involved.

The textual application is manifest. *The greatest mixture of germ plasm is going on, but no single hereditary factor or determiner is altered in the process, and has not altered throughout the history of ostrich breeding; only new combinations are formed of factors already available.* The farmer himself has long grasped this and does not look for any change; he knows he can get nothing beyond what the wild bird had to start with; he can create or change nothing, beyond what can be ascribed to good management and feeding. For practical purposes his understanding of the individuality and fixity of the germ factors producing the plume is as clear as that of the most zealous Mendelian; but only in a few instances has he ever heard of the factorial hypothesis, though facts upon which it could have been established were discovered in his farming practise long before 1900, the year of Men-

delian reawakening. If his birds, judging by their feather performance, are lacking a certain germ factor he is well aware that he can by no possible means originate the factor nor hope to produce it in any way; he must procure it from some other farmer whose birds display it, and then he may expect to secure it in combination in his own strain.

III

"Selection only acts as a mechanical sorter of existing diversities in the germ plasm and not as a cause of alteration in it."

The term "selection" is employed by the ostrich breeder in South Africa with all that freedom which Pearl finds among the plant and animal breeders in America, but he is never under any delusion that it signifies more than is implied in the simple meaning of the word. He has retained its plain everyday significance and the majority have never heard of Darwin and "The Origin of Species by Means of Natural Selection," nor of the extended meaning which students of evolution are inclined to give the term, as in the phrase, "The Selection Problem." To the ostrich farmer "breeding from selection" simply means that for his breeding sets he picks out birds having the special plumage characters he desires to see in their progeny, or which he expects to get from the combination of the cock and the hen. Selection is merely used in contrast with indiscriminate breeding, as where any cock and hen may be camped off without regard to their plumage value, or in contrast to breeding on the veld where any cock may mate with any hen. He selects partly on the basis of somatic performance and partly on proved germinal production; many birds which themselves give indifferent plumage are yet employed as breeders from being known to produce superior chicks.

From his life-long experience in selective breeding the ostrich farmer clearly grasps that all he is doing is to sort out birds from among his flock with certain characters

which he desires to see in combination in their progeny, but he never dreams that any change in the characters themselves will result therefrom. Though perhaps unable to express it in words he knows that the germ plasm of each of his birds contains so many factors, and in his selection of breeders picks out the birds having the factors he desires to give him new combinations, but he has no expectancy that the factors themselves will undergo any change as evidenced by their expression in the progeny. Selection along the prescribed lines is probably as rigid as that which any experimentalist could carry out, and is certainly more so than can be conceived of as taking place in nature, yet long as it has been in operation it has never carried with it an alteration of any of the existing diversities of plumage.

IV

"When the germ plasm changes it does so as a result either of wholly internal physiological causes, or of very extraordinary environmental stresses acting directly upon the germ cells."

The bodily characters of the South African ostrich present a remarkable uniformity except as regards certain details to be described later, but in comparison with the North African bird many striking differences appear. In 1912 the Government of the Union of South Africa imported 132 specimens of the northern ostrich from Nigeria. It was hoped that in these some one or other of the plumage characteristics might be developed to a higher degree than in the southern bird and could with advantage be combined with the latter. Experiments with this end in view are now in progress under the direction of the writer.

The northern ostrich is longer in the legs and neck than the southern, the head reaching a little over eight feet from the ground, about a foot more than in the latter. The color of the skin of immature birds of both sexes and of mature hens is a creamy yellow, while the mature cock

is bright red or scarlet on the legs, head and neck, and red and pink over the body generally; in the southern ostrich the skin of the neck, body and legs is a pale yellow in chicks, dark gray in mature hens and dark blue in cocks, while in the sexually ripe cock only the beak, the front part of the head, the naked skin around the eyes and the tarsal scales are a bright scarlet. The crown of the head of the northern bird has a bald oval patch while that of the southern is covered with hair-like feathers similar to those over the rest of the head and neck. The northern egg is larger and rounder, with an enamel-like smoothness, and is practically free from obvious pittings; the southern is deeply pitted all over, smaller and more oval. Knowing as we do the habits and life of the ostrich it is in the highest degree improbable that any of the differences have an adaptive significance or selective value in nature.

When the birds are observed side by side, as can now be done at Grootfontein, the above characters readily serve to separate the northern from the southern ostrich, and may well be held to justify the specific distinction usually accorded them. That the distinguishing features of the former are not environmental but germinal is proved by the fact that they persist under southern conditions and have reappeared in progeny already reared. Numerous cross-breds or hybrids of the first generation have also been obtained, but sufficient time has not yet intervened to secure the second hybrid generation. As regards dimensions, color and the nature of the egg the first generation of cross-breds are intermediates in varying degree between the northern and southern parents, but the bald head patch of the northern is dominant over its absence in the southern, appearing in all the crosses yet reared.

It is clear that the germ plasm of the northern ostrich has undergone marked changes compared with that of its southern representative, or *vice versa*, for one can only think of the various races or species of *Struthio* as derived from a common stock. In terms of the sectional heading we may well enquire whether the changes are due to

internal physiological causes or to extraordinary environmental stresses acting upon the germ cells. We have already seen that germinally the South African ostrich is most irresponsible to any environmental changes and we have no reason to suspect that its northern relative is in any way more impressionable. In the climatic and other environmental conditions of North Africa it is difficult to conceive of anything which could, for example, modify the bodily colors as compared with those of the southern bird, or could bring about a perfectly smooth round egg in contrast with an oval pitted one, much less which could either directly or through the soma change the germ cells so as to render the differences hereditary. Of course we know next to nothing of the influence upon the germ cells of extraordinary environmental stresses and to labor the point would be unprofitable. But doubt may certainly be expressed as to whether any external influence could so change them as to bring about the formation of a bald head patch, a feature which it is impossible to regard as having an adaptive significance. It is a new germinal character which has appeared in the northern bird, entirely *sui generis*; there is nothing suggestive of it in the southern ostrich.

We have the hard fact to account for that the germ plasms of the northern and the southern ostrich differ from one another in certain respects as revealed by their manifestation in the soma, and it is also proved that they breed true irrespective of environment. And while in our condition of absolute ignorance no good purpose will be served by dogmatizing it may be permitted to express the conviction that the germ plasm changes as between the northern and southern ostrich have resulted entirely from internal physiological causes. The conviction is strengthened all the more from the facts to be presented in the next section.

B³

V

"Hereditary determiners or factors fluctuate regularly and frequently, if not indeed usually, and in high correlation with somatic characters."

In a certain measure this statement may be looked upon as opposed to that with which section 1 opens, but no one would maintain either the one or the other to be the exclusive state of the germ plasm, hereditary determiners or factors of all animals and plants. We have abundant evidence that the germ plasm is remarkably conservative for some forms of life (persistent types) while in others it may fluctuate or change frequently (*Drosophila*); also, it is not unreasonable to expect that at any one period the factors for certain parts of an organism may remain fixed while for others they may be in a state of change. We have seen that the factors controlling the structural details of the ostrich plume are peculiarly constant, but the endeavor will now be made to establish that those for the wing feathers numerically, as well as for certain other parts of the bird, are undergoing regular and frequent changes and in determinable directions.

By zoologists the wing of the ostrich is usually regarded as degenerate, on account of its small size compared with the body and legs and the practical absence of any covering of feathers on its inner or under surface. Certain studies recently made have given good reason for concluding that in many other less obvious respects it is still undergoing degeneration. The full details upon which

³ The three statements under section B are obviously considered by Dr. Pearl to apply specially to Dr. Castle's claims in connection with his experiments on piebald rats, a condensed account of which appears in the same issue of the NATURALIST as Pearl's paper (p. 102). Instead of regarding them as applicable only to the disputed plus and minus fluctuations in the factor itself it may be permissible to consider them in a broader sense, as referring to the nature of the germ-plasm generally and as contrasted with those in section A. What follows has probably no connection with results such as those which Castle has obtained but nevertheless it is hoped to show that real factorial changes, continuously retrogressive in their nature, are going on in the germ plasm of the ostrich and that there is much likelihood the changes can be influenced by selection.

the claim is based will appear later. Only the outline of the facts can now be given in so far as they bear upon the condition of the germ plasm.

Only a single row of under-coverts usually occurs on the wing of the ostrich, its members alternating with the remiges or wing quills (Fig. 1). In but two specimens out of hundreds examined however has the full number of feathers required for alteration with the complete row of remiges been found. Usually eight to ten are missing from the elbow end of the row, though the number varies, and occasionally two or three vestigial feathers may appear between the normal members and the missing sockets. Single plumes are at times met with in front of the row and are obviously representatives of a second row, while in one farmer's strain an almost complete second row of under-coverts occurs, alternating with the first, and in front of this are five or six members of a third row. One is forced to the conclusion that the ancestral ostrich had the under surface of its wings provided with several rows of under-coverts in the same manner as modern flying birds, and that the rare occurrences mentioned are in the nature of survivals, the germinal factors responsible for their appearance having been largely, though not yet altogether, lost to the race.

The valuable wing quills or remiges ordinarily vary from 33 to 39, having the same average, about 35.5, for both the northern and southern birds. They constitute a fluctuating series about the mode 36, though there is much probability that each separate number in the series will be found to represent a pure line. Assuming that not much numerical variation occurs in the plumes of the ostrich the farmer has never yet bred for quantity, quality has been his only consideration. Recently however a cock bird has been discovered among the government's experimental troops bearing 42 remiges, and it is submitted that this high number represents an ancestral survival rather than a reversion or mutation, and that the wing quills of the African ostrich afford us various stages in degenera-

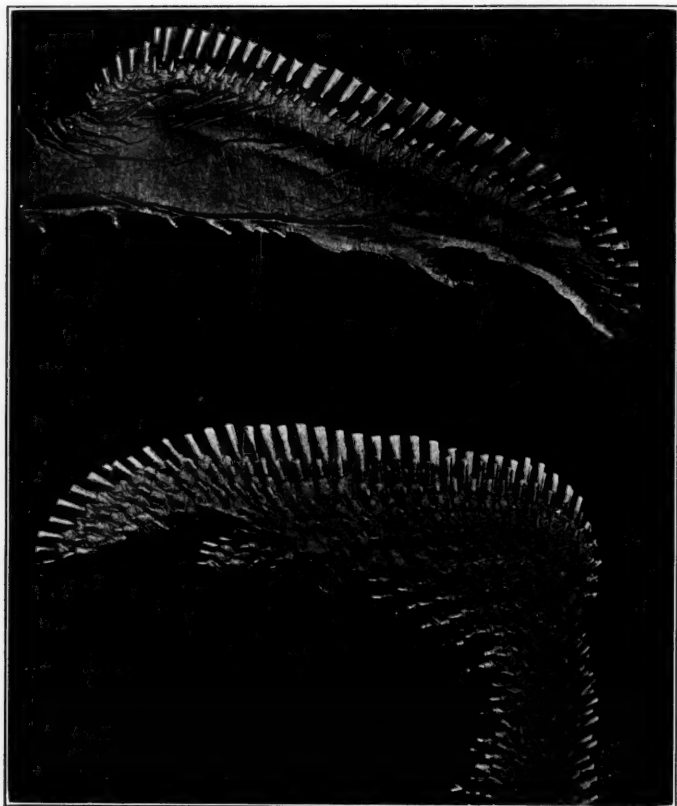


FIG. 1. Under surface of wing of ostrich with plumes clipped off. In by far the majority of ostriches the surface is naked except for the single row of under-coverts which is rarely complete; in the specimen represented six of the coverts are missing from the elbow end of the row. In one farmer's strain an almost complete second row of under-coverts occurs and also a few members of a third row. The third digit is almost buried in the flesh of the wing, but can be seen projecting slightly towards its distal end. The claw which is present on the first and second digits is not clearly shown.

FIG. 2. Outer surface of wing of ostrich, the plumes having been clipped off to show their arrangement in rows. The feathers in the uppermost row, the wing quills or remiges, vary from 42 to 33 in different birds. The members of the first row of upper-coverts alternate with the wing quills and vary with them in number, while the second row of coverts has often a number missing towards the free end of the row, though not in the wing represented. The other rows of coverts, third, fourth and fifth, may also show reduction. The marginal row of the bastard wing may contain from two to seven feathers.

tion from the maximum 42 to the present minimum of 33. As experiments have proved that the high number breeds true, and as the other rows of commercial plumes vary in correlation with the remiges, the discovery has a great industrial bearing; for it now becomes possible to provide the farmer with a pure line of 42-plumed ostriches in place of the degenerate 36-plumed birds with which he farms to-day, and the entire feather crop will surpass the present one by about 25 per cent.

The first row of upper-coverts varies in correlation with the remiges (Fig. 2) but never shows any independent reduction, while the second row has often a number missing from its distal end, and is clearly undergoing reduction here in contrast with the elbow end for the under-coverts. Again, it is usually stated by writers that the ostrich is destitute of an under-covering of down feathers and filoplumes, yet in every northern and southern bird examined, down in all stages of degeneration occurs around the base of the larger plumes of the wing and tail, and in rare cases spreads over a wider area, leading to the conclusion that at one time the ostrich had an under-covering of small feathers like flying birds generally.

The third digit displays certain most unexpected evolutionary stages. While in most cases it is altogether embedded in the flesh of the wing, and can only be seen and felt through the thin skin, yet occasionally its tip projects quite freely, suggesting its former separation, like the first digit which forms the ala spuria. Moreover, in some birds odd feathers are to be found set along the finger, altogether detached from any other series. These are surely to be understood as survivals of a time when the third finger was clawed, free and provided with its own feathers, a primitive condition which is usually held to be represented only in the oldest known fossil bird, *Archaeopteryx*.

The legs and toes likewise exhibit degenerative phases. The African ostrich is unique among living birds in hav-

ing already lost its first, second and fifth toes, only the third and fourth remaining. The outer, fourth toe is far smaller than the inner third toe, and the condition of its

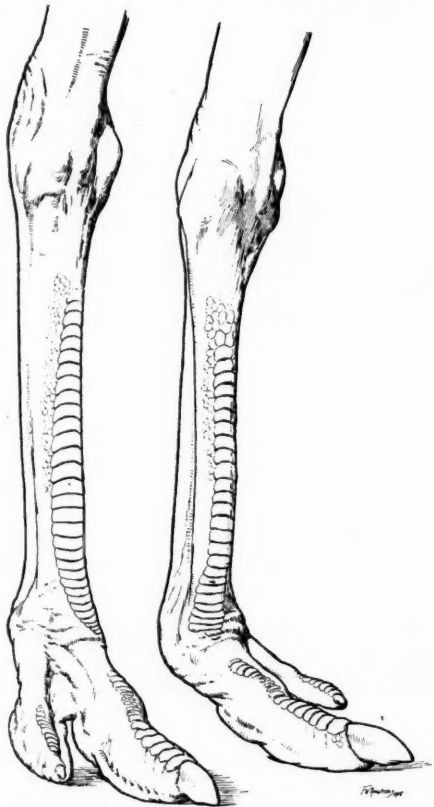


FIG. 3. Tarsus and foot of North African ostrich. The outer, fourth toe is greatly reduced in comparison with the inner, third toe. The former shows a small non-functional claw. A distinct break occurs between the scutellation of the tarsus and that of the middle toe, though in most ostriches the two series of scales are continuous. A second break is beginning to form over the middle joint of the toe, the larger scales being divided into two or three smaller ones.

claw as well as its smaller size lead one to infer that it also is on the road to disappearance (Fig. 3). In northern birds the claw of the fourth toe is frequently discernible, though altogether functionless, never reaching the ground;

but on only a few southern birds is it ever seen, and then in a most vestigial state, barely showing beyond the skin.

What may doubtless be regarded as the first steps in the degeneration of the big middle toe are also displayed. Down the front of the tarsus extends a series of large, nearly rectangular scales, continuous all the way from a little below the ankle and passing over the upper surface of the toe, though usually somewhat smaller where the toe joins on to the tarsus. In a few ostriches a distinct break occurs at the joint, several large scales being altogether wanting (Fig. 3), and rarely birds are met with in which a second break takes place over the middle joint of the toe. One may hazard the suggestion that the interruption in the scutellation over the two joints has an adaptive significance, allowing the parts to move more freely, but we have also to face the fact that the single break occurs in but a few while the double break is very rare. It is presumably a new feature in course of introduction into the ostrich race, but not yet established for the members as a whole. It involves however a reduction in the make-up of the toe; it is a minus or retrogressive mutation, and may well be the first hint of impending loss of what will be the only toe when the small fourth has gone.

Although definite experimental data on all these reduction phenomena are not yet available everything points to the fact that the variations breed true and are therefore germinal in their nature; they are certainly not ordinary fluctuating somatic variations. Proof is to hand that the 42-plumed cock has factorial representation for its high number of plumes. Another similarly numbered hen is not yet available, but in crosses with various 36-plumed hens the average number of plumes of the progeny is 39.56 which is midway between the parents, while the mode is 40. Considering the heterozygous nature of the ostrich where number of plumes is concerned a fluctuating series of this kind is what would be expected. Only one farmer's strain has the nearly complete second and third rows of under-coverts, but they are found in all the progeny from

the strain; all the members of a flock bred from the same stock have the second row of upper-coverts complete, while in other flocks all the members have a number of plumes absent from the row. Crossing of birds in which the complete loss of the claw on the small toe has taken place with others in which the claw still appears gives results on strictly factorial lines, as also does the crossing of birds with and without a loss of the scales. In a mixed assemblage of any species where only a small proportion display a certain character it may be presumed that the latter will be heterozygous with regard to the particular character, seeing that the chances are much against the mating of two individuals each having the character. The heterozygous nature of the bird can be demonstrated on mating with one in which the character is absent, for if dominant it will appear in half the progeny and be absent from the others. This proportion with regard to the presence of the claw and the loss of the toe scales has been found to hold in all the crosses. Out of a total of 36 chicks hatched from breeding pairs where one parent was clawed and not the other the numbers were actually equal, namely, 18 chicks were clawed and 18 unclawed. Out of 11 chicks reared from a pair where one parent showed no loss of scales on the big toe and the other had a single break, 5 had no break and 6 showed the break.

It may be accepted then that all the degenerative phases represent factorial changes which have come about in the germ plasm of the ostrich. Presumably the changes involve a loss of factors; they are retrogressive or negative mutations. Structures which would be expected to occur either fail to appear or are seen very rarely, and may then be regarded as survivals, the factorial losses not having yet taken place in the particular individuals. Thus, to take the case of the first row of under-coverts, the principle of alternation demands that a complete row of under-coverts should alternate with the row of remiges. The full row actually occurs in a few individuals, and

suffices to prove that this was the condition in the ancestral ostrich; more usually eight to ten are missing and also fail to appear in the progeny. It is therefore reasonable to assume that the germ factors originally involved in the production of the eight to ten under-coverts have disappeared from the majority of ostriches though they are retained in a few. The fact that all the intermediate numbers can yet be obtained shows the loss to have been progressive. A similar line of argument can be applied all through. Loss or degeneration is in progress in various directions and differs in degree in different individuals, and the losses are the outward expression of internal changes in the germ plasm.

Where a loss of factors is taking place it could hardly be expected that all the individuals of the race would be affected at one and the same time. The process would be more rapid in some than in others, some would incur the loss at one time and some at another, and the results from crossing would need to be reckoned with. Hence we can understand the great diversity of stages represented in the ostrich where large numbers are available for examination. It may be hard to comprehend how in the first instance germinal changes can be brought about, but if once effected, their repetition and continuance can reasonably be expected. Beginning with one or a few birds it is manifest that as the loss in any direction continues more and more individuals will become affected, until in the end complete loss for the race will be achieved. So far as the investigation of farmer's troops has proceeded it affords strong evidence for the view that only one original 42-plumed bird now exists in South Africa, so that under natural conditions the extinction of this high number of remiges would be imminent. The loss of the claw from the third finger is probably only recent. Some textbooks of zoology⁴ assert that a third claw occurs, but it has never been found on the hundreds of southern and northern ostriches coming under my examination, although specially looked for.

⁴ Parker and Haswell, Vol. II, p. 393.

In most instances it would appear as if the loss of all the many factors concerned in the production of a single plume takes place simultaneously, as is the case with most meristic structures; for usually the absences are complete plumes. In some birds, however, two or three incompletely formed or vestigial feathers occur between the normal feathers of a row and the absent sockets, as if the loss of the individual plume were taking place piecemeal. This condition can be easily understood if we assume that the constituent factors concerned do not all drop out together, but follow some sort of succession. The factors left at any time would then give rise to the part of the feather for which alone they are responsible, and we should get an imperfect or vestigial feather. In any animal vestiges of a structure will continue to appear so long as any of the factors concerned in the original structure remain. It is submitted that degeneration of any complex structure never takes place in a gradual continuous manner, as is usually supposed, but by successive steps determined by the manner in which the factors drop out; the appearance of continuity will however be conferred if the steps are small enough.

If a sufficient number of individual ostriches were gathered together it could easily be made to appear as if degeneration in any of the recognized directions were taking place in a slow continuous manner, for all stages between the extremes could be obtained. Proceeding by such a method however would give an erroneous impression of what is actually happening. For although all stages do occur they are in reality disconnected, and each stage has been reached in an individual quite irrespective of the others, and represents a separate and distinct germinal loss; furthermore, in the same individual degeneration in any one direction proceeds quite independently of the other directions in which the process is taking place. It is not the wing as a whole which is undergoing degeneration, but the constituent parts of which it is made up, each presumably represented by its own factors and be-

having with a large measure of independence. The losses are continuous for the race but discontinuous for the individual; and it is with the individual that heredity is concerned and evolution with the race.

The degeneration phenomena presented by the ostrich in connection with its wings and legs, as well as with its plumage, would appear to provide us with an example of the application of mutative and Mendelian principles to such evolutionary facts as confront the comparative anatomist and paleontologist. So far as concerns the individual bird the retrogressive changes are shown to occur as separate mutations and to follow definite factorial lines, while as concerns the evolution of the race they proceed in a continuous determinate manner. In all probability they take place wholly irrespective of any adaptive significance or consideration for the welfare of the bird, and are intrinsic in their nature and uninfluenced by external conditions. Natural selection has probably played no part in connection with the losses, for the greater changes have already affected the race uniformly and the smaller ones which still vary in degree in different individuals will probably affect the whole in the end. Should the loss of plumage continue to a much further degree and marked degenerative changes be set up in the big middle toe natural selection may then be expected to bring about extinction.

The chief point desired to establish at present is that as regards the number of its wing plumes and in certain other features the ostrich affords strong support for the view that its hereditary determiners or factors are changing regularly and frequently; they are not fixed and constant as are the factors for the structural details of the plumes; one series is in a state of change, the other is non-changing. The great variety and degree of the degenerative stages in the ostrich of to-day admits of no question, and that they are the expression of so many germinal differences may be accepted, seeing that they breed true; that they have been effected simultaneously as we find

them is inconceivable, and we are justified in concluding that in the past the germ plasm has changed frequently and presumably over a long period. Moreover, we can hardly admit that the various degenerative phases will remain as they are at present, but that further losses in the same direction will follow, that is, the germ plasm will continue to undergo retrogressive changes of a like character to those already initiated. We may have an appearance of continuous change, but when analyzed it will be found to proceed by means of separate factorial steps. It is conceivable that a continuance of the kind of factorial losses now in progress will result ultimately in the complete disappearance of the wings and legs of the ostrich, allowing that the bird could survive the intermediate stages, a postulate which it must be conceded is of no mean order. May we not suppose that the limbless condition of snakes and some lizards, amphibians and fishes has come about by the successive losses of germinal factors in a similar manner to that which is here shown to be taking place in the ostrich?

The bearing of the germinal changes involved in the degenerative processes upon the thesis of Section IV, may be noted. It is in the highest degree improbable that determinate losses of such a widely embracive nature are taking place in response to any environmental stress acting upon the germ cells; rather they may be regarded as the result of some wholly internal physiological cause. If due to environmental stress one could reasonably expect that in any individual the losses would be taking place in all directions simultaneously, and would have reached about the same degree in all. But among the various rows of feathers, as well as in other parts, the greatest independence in reduction is met with, as if the factors for each were subject to a separate rather than a common influence.

VI

"Mixing of germ plasms in fertilization alters hereditary determiners mutually and hence is, in and of itself,

a cause of genetic variations . . . a purely external agent, the continued selection of personal somatic qualities, will alter the germ plasm."

It seems to be generally allowed that at any period the majority of forms of life are static so far as germinal alterations are concerned, while some are undergoing progressive changes and others retrogressive changes. During the present period the representatives of the widely distributed *Ratitæ* are unquestionably undergoing marked changes and have been for ages past. The changes are in a negative or retrogressive direction, and express themselves in somatic degeneration, particularly with regard to the wing and shoulder girdle. The living *Apteryx* is a well-known instance of wing degeneration, as also the recently extinct moas, in which no hint of a wing has been found and a trace of the glenoid cavity only in one species. From the data already submitted we are able to learn something as to the manner in which the degenerative processes are proceeding in the wing and leg of the ostrich, and presumably the same method holds for the *Ratitæ* generally. Factors are evidently in process of dropping out, in regular succession, along definite prescribed lines, the degree varying much when the entire race is taken into account.

All Mendelian writers seem to concede that the factorial changes, plus or minus, are not autonomous on the part of the factors, but are "a result either of wholly internal physiological causes, or of very extraordinary environmental stresses acting directly upon the germ cells." Though the results of Morgan and his associates indicate that it may yet be possible to understand the manner in which the factors undergo their changes it will always be competent for us to enquire as to the cause or causes inducing the changes. To be complete our analysis of variability will need to get beyond the factors to the force or forces acting upon them. In the previous sections good reason has been adduced for supposing that the losses going on in the germ plasm of the ostrich are

due to some wholly intrinsic cause, and seeing that it affects all the members of the race and has been operative for a long period we may conclude that it is transmissible and acts continuously from generation to generation. The many stages represented also give some justification for supposing that whatever the cause of the factorial changes may be it varies in intensity in different members of the race, being less active in individuals where the loss of plumes is small as compared with others in which the loss is greater. For example, the causative agent bringing about the loss of the plume factors must be less in intensity or less active in 42-plumed ostriches than in 33-plumed birds. We may with good reason expect that the selection for breeding of the high numbered birds will arrest the rate of degeneration of the race in this particular feature, while on the other hand the selection of the low-numbered birds will tend to accelerate the rate at which the factorial losses are taking place. Where therefore the germ plasm of a race is in a continuously changing phase, as in the ostrich, we can hope to retard or accelerate the changes by selecting individuals differing in the degree to which they are under the influence of the causative agent. It is submitted that in this sense we can say that "a purely external agent, the continued selection of personal *somatic* qualities, will alter the germ plasm."

We can not hope that the continued selection of 42-plumed birds will in the end give to the farmer ostriches with a still higher number of remiges, as the factors for the plumes beyond these have in all probability disappeared from the race, and there is no evidence that the cause of the factorial changes is effective in a plus but only in a minus direction. On the other hand the continued selection of 33-plumed birds may reasonably be expected to accelerate the loss of the remiges, by leading to a more rapid loss of the factors. Owing to the present degenerative forces at work in the ostrich we can by selection hope to modify the germ plasm in a minus direc-

tion, though not in a plus direction, beyond the present limits of the race. It will of course be readily appreciated that this possibility differs altogether from that due to the ordinary selection which may go on in a race of organisms where the germ plasm is static, but where all grades of pure lines may be extracted between extreme limits. Where the germ plasm for a race is static, as demonstrated by Jennings in his work on *Paramæcium*, we can readily understand that no further change is possible by selection within a pure line, as nothing inducing factorial changes is present. If where germinal changes are taking place it is not permissible to think of the factors as changing autonomously we have to assume that some causative agent is present, and may vary in degree in different members and thereby form a basis for selective action.

The same considerations can be applied to the statement: "mixing of germ plasms in fertilization alters hereditary determiners mutually and hence is, in and of itself, a cause of genetic variations." When, for example, two germ plasms, in each of which the causative agent producing loss of factors is at its maximum, become mixed in fertilization it is reasonable to expect that the agent will be intensified and the hereditary determiners will be altered mutually, and some of them drop out. The mixing will be, in and of itself, a cause of genetic variation, which will be expressed by a further loss of remiges.

Though the idea of a causative agent inducing changes in the germ plasm, and varying in degree and also transmissible, is altogether hypothetical yet it is stimulating to further experimental effort. Of the hundreds of ostriches examined not one has been found with less than 33 remiges, hence this number must be regarded as the present minimum of the race. There is every reason to expect that a pure line having this number only can be built up. If by breeding these together a further reduction of plumes should take place we should then be fully justified in assuming that the factors concerned with the

lost members had dropped out from the germ plasm, especially if later breeding failed to restore them; selection would have induced a definite change in the germ plasm. Also if a pure line with 42 remiges were established and no further increase occurred we should be warranted in concluding that the factors for the plumes beyond this number had already disappeared from the race and could not be restored; the causative agent could not act in a plus direction. It is unfortunate for such investigations that the ostrich is such a slow breeder. Experiments are however being conducted to determine if further reduction in the 33-plumed birds can be induced, while the building up of a pure 42-plumed race is also in progress, the latter having an important industrial bearing.

In many respects the degeneration phenomena in the ostrich appear to be best understood on the conception of autonomous changes and variations in potency of the germ factors. In the case of the dropping out of plumes during the chick stage the reduction in potency has proceeded so far as to result in entire loss of effectiveness only from the chick stage onwards, while complete loss of factors from the germ plasm may be regarded as the final loss of potency. May not a variation of potency of factors be at the root of many of the so-called fluctuating variations? The explanation seeks for the loss of factors among the autonomous changes in the factors themselves, while the idea of a "causative agent" throws the responsibility for the changes upon some influence external to the factors.

Since the above was written certain results have been obtained which strongly support the idea that it may be possible to induce retrogressive changes in the ostrich. As stated, a loss of scales over the large middle toe has already taken place in a small proportion. Out of twenty southern birds of mixed breeding one showed a single break while out of twenty mixed northern birds a single break occurred in three cases and a double break in two. The results given below are derived from the mating of a

northern cock without any break and a southern hen in which the break occurs. Of the four offspring reared three are without the break while it occurs in hen No. 179. From the mating of brother and sister four F_2 chicks were hatched, two of which have a double break in the scutellation, one shows a single break and one has no break. Thus the proportional loss of scales has greatly increased in the F_2 generation.

SCUTELLATION IN F_2 CHICKS COMPARED WITH PARENTS
AND GRANDPARENTS

	No Break	Break
N. A. cock, No. 9.....	×	—
S. A. hen, No. 225.....	—	×
<i>F. Crosses.</i>		
Cross-bred cock, No. 182.....	×	—
Cross-bred hen, No. 179	—	×
<i>F₂ Chicks.</i>		
No. 1	—	××
No. 2	—	×
No. 3	—	××
No. 4	×	—

From what has been adduced already we may with good reason admit that an inherent tendency exists in the ostrich towards the loss of certain parts of the fore and hind limbs, and the above result may be regarded as highly suggestive that by inbreeding the inherent tendency towards the loss of scales can be accentuated along definite lines. The accumulation of fuller data must be awaited before the suggestion can be regarded as more than tentative.

ADAPTATION AND THE PROBLEM OF "ORGANIC PURPOSEFULNESS." II

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IV. THE PRINCIPLE OF TRIAL AND ERROR IN RELATION TO REGULATIVE PHENOMENA¹⁴

Driesch and some other vitalists draw their most effective ammunition from the phenomena of experimental embryology and regeneration. How is it that a fragment of a developing organism—any fragment, within certain limits—can produce the whole? How is it that various perversions of the normal course of development do not prevent the attainment of the normal end? How is it that certain adult organs, *e. g.*, the lens of the eye of a triton, when removed by a highly "unnatural" operation, is nevertheless restored, and restored by a process quite different from that in which it is normally produced in embryonic development?

At the outset we must make two admissions: (1) that these processes can not be the result of a mechanism specifically adapted in advance to meet these particular exigencies, and (2) that they can not be satisfactorily explained by assuming any preformation of the parts which are restored. The former supposition is to be re-

¹⁴ The "trial and error" principle has of late years come into the foreground of biological discussion, largely through the writings of Jennings. It was, so far as I know, first clearly proposed (though not so named) by Spencer (*Principles of Psychology*, Vol. I, pp. 544-545) to account for the origin of adaptive responses to stimuli, and was later developed by Bain. There are important points of agreement between the views of these writers and some of those set forth independently by Roux in his classic essay, "Der Kampf der Theile im Organismus" (1881). More recently, Baldwin (*Mental Development*, 1898, Chapter VII; *Development and Evolution*, 1902, pp. 108-115) has further elaborated the same fundamental idea as that of Spencer and Bain in his theory of "functional selection." Various animal psychologists (*e.g.*, Lloyd Morgan and Thorndike) have also laid stress on this principle.

jected on account of the unusual and artificial character of the operations, which could never have been provided for by natural selection, nor, so far as we can see, by any other recognized principle of evolution. The latter supposition is sufficiently disposed of by Driesch's analysis (section III) and need not be considered here.

Driesch admits that a physico-chemical machine "might very well be the motive force of organogenesis in general, if only normal, that is to say, if only undisturbed development existed, and if a taking away of parts of our systems led to fragmental development" (II, 139). If, therefore, we can explain these critical cases without invoking any principles beyond those believed to be operative in normal life-history, we have disposed of this line of argument.

In an earlier section of this paper I took the ground that an adaptive or "purposive" response by the organism, if not guided by past individual or racial experience, must be the result of experimentation. I avoided intentionally at the time any consideration of those cases of regeneration and form regulation in which the emergency was totally new, and therefore foreign to the experience of the organism or its ancestors. Here a specially evolved mechanism could hardly be invoked. I suggested, however, that the principle of "trial and error" could be applied to these cases. This suggestion was, of course, not new. Such an extension of this conception had already been made by Jennings,¹⁵ though it is rather surprising to note that he has given it little further consideration in his recent discussions of vitalism. For, to my mind, an explanation involving this principle, seems the only alternative at present to a vitalistic one, or, better stated, it seems to me the only alternative to an abandonment of the search for a scientific explanation.

According to the trial and error principle, as applied to the movements of a lower animal, "behavior that results in interference with the normal metabolic processes

¹⁵ "Behavior of the Lower Organisms" (1906), Chapter XXI.

is changed, the movement being reversed, while behavior that does not result in interference or that favors the metabolic processes is continued."¹⁶ The primary "avoiding reaction," in the presence of an unfavorable stimulus, is, of course, comparable with a simple reflex. Its ordinary effect is to remove the organism from the noxious influence. When progressive movements are resumed, they occur at random, so far as their direction is concerned, and they may or may not take the organism into favorable surroundings. If they chance so to do, they are continued indefinitely. If not, the reversal of movement occurs as before. Thus while, to the uncritical observer, the organism seems to "seek out" the optimum environment, it really reaches this through a series of accidents. This is as true of a cat, releasing itself from an experimental trap, as it is of a paramoecium escaping from a harmful to an optimum water temperature. In the case of the cat we may be tolerably sure that the animal experiences a feeling of discomfort until the means of escape is discovered, and we find it convenient, if not inevitable, to say that her restless movements are the *result* of this feeling. In the case of the infusorian, we are much less sure of the conscious element, though its introduction is permissible as an act of philosophic faith. In theory, most scientists are probably psychophysical parallelists, but in practise it seems necessary at times to use the language of interactionism. In discussing the voluntary movements of a higher animal, any other course would seem pedantic. But in discussing the simple behavior of a lower organism, such language is commonly branded as "anthropomorphic." Nevertheless, I believe that its employment even here is sometimes useful in forcing us to keep in view the essential unity of animal life. No protest is raised by the physiologist when thoroughly *protozoomorphic* language is applied to a vertebrate. Why then should "anthropomorphic" terminology so shock us in describing the be-

¹⁶ Jennings, *op. cit.*, p. 39.

havior of a *Paramæcium*? Each is the extension of an article of philosophic faith far beyond the realm of experience. But this is no essential part of our present argument. Let us consider whether the trial and error principle may not be applicable to other phenomena than the bodily movements of animals.

Jennings asks:

Is it possible that interference with the physiological processes may induce changes in other activities,—in chemical processes, in growth, and the like,—and that one of these activities is selected, as in behavior, through the fact that it relieves the interference that caused the change? . . . It is evident, then, that the organism has presented to it, by the condition just sketched, unlimited possibilities for the selection of different chemical processes. The body is a great mass of the most varied chemicals, and in this mass thousands of chemical processes, in every direction,—all those indeed that are possible,—are occurring at all times. There is then no difficulty as to the sufficiency of the material presented for selection, if some means may be found for selecting it (*op. cit.*, p. 346).

Looking for evidence that such a process of selection does actually occur in physiological regulation, Jennings cites the experiments of Pawlow, in which the latter habituated dogs to various kinds of foods and noted the effects upon the digestive juices. In these experiments the adaptive changes in the activities of the digestive glands, fitting the digestive juices to the food taken, do not occur at once and completely under a given diet, but are brought about gradually. . . . This slow adaptation is, of course, what should be expected if the process occurs in anything like the manner we have sketched (p. 347).

Jennings concedes:

It is perhaps more difficult to apply the method of regulation above set forth to processes of growth and regeneration. Yet there is no logical difficulty in its way. The only question would be that of fact, whether the varied growth processes necessarily do, primitively, occur under conditions that interfere with the physiological processes. When a wound is made or an organ removed, is the growth process which follows always of a certain stereotyped character, or are there variations? It is well known, of course, that the latter is the case. . . . Removal of an organ is known to produce great disturbances of most of the processes in the organism and among others in the process of growth. . . . Some of these relieve the disturbance; the variation then ceases and these processes are continued (p. 348).

A line of argument which has points of similarity to the foregoing has been independently developed by Holmes.¹⁷ He believes:

The harmonious functioning of an organism is mainly secured by a system of automatically acting checks which we may conceive to act in manner more or less remotely analogous to the governor of a steam-engine or the forces which regulate the motions of the planets. . . . In these cases deviation from the normal is the cause which automatically sets up activities by which the normal is regained.

So, too,

the self-regulation of organisms may . . . be in a measure understood if we assume that their parts stand in a relation of mutual dependence such that the undue growth or functioning of any part is held in check by the reactions thus brought about by other, and especially the contiguous structures. If we suppose that the various cells constituting the body have each a different kind of metabolism, and that the products of each cell are in some way utilized by the neighboring cells, so that each derives an advantage from the particular association in which it occurs, we may understand, in a measure, how this checking may be brought about.

And here an analogy is pointed out with the relations which obtain in "symbiotic" communities, such as those composed of animal cells and certain unicellular algæ.

The conception here developed is in some respects an extension of Roux's intra-selection hypothesis, though Holmes rejects the notion of a "struggle of the parts." This conception, which derives strong support from recent discoveries respecting "hormones," gives a certain measure of concreteness to that rather vague expression, "the organism as a whole." For, despite the many known instances of local autonomy, we can not doubt that the organism does in a high degree act as a whole. But this "wholeness" may not be an irresolvable fact, as has sometimes been assumed. It may be possible to conceive it in terms of chemical and structural integration.^{17a}

This hypothesis, as applied to form regulation, would

¹⁷ *Archiv für Entwicklungsmechanik*, 1904.

^{17a} To me, such a viewpoint seems quite reconcilable with the "organismal" conception of Ritter, though Professor Ritter himself (*The Unity of the Organism*, Vol. I, p. 183) has gone to considerable pains to show the fallacy of Holmes's position.

seem to be closely related to that of Jennings, and indeed Jennings himself views it in this light. It is difficult to gather, however, to what extent Holmes has in mind the principle of "trial and error." His comparison of regeneration with functional hypertrophy does not seem compatible with this principle. "Remove one of a pair of organs," he says, "and its fellow increases in size. Remove a part of one of these organs and the remaining portion grows, forms new tissue, and regenerates the missing part." Furthermore, he believes that these phenomena may be analogous with some of those described under the name of "chemical equilibrium."

The decomposition of compounds in solution proceeds until there is a definite relation established between the amounts of the old compounds and the new. If the chemical equilibrium thus established is disturbed by the removal of one of these compounds more of that compound will be produced; and the more rapidly the compound is removed, the more rapidly it is formed.

Such an "automatic" restoration of equilibrium as this might seem to be a radically different thing from trial and error. The process by which it is attained would appear to be direct and unhesitating. Holmes says that the solar system, no less than the organism, is a "self-regulating mechanism." Now, in the former, the balance of its opposing forces is effected "automatically" in the sense that any deviation in the movement of one of the parts would result inevitably in a compensating deviation in the others. Is the restoration of an organism to its norm of this direct and automatic type? Are such processes as tend to compensate a disturbance in the normal functioning of an organism the direct and exclusive result of the disturbance itself, or does this disturbance evoke a variety of responses of which the suitable response may finally happen to be one? The first of these alternatives may be admitted as probable in the case of such disturbing factors as have been frequently experienced in the past. But how does it happen that certain cells of the iris of a newt become stimulated to division by the removal of the lens? And why should

their metabolism become so affected that they give rise to lens tissue, instead of to iris tissue? Can we believe that the iris cells proceeded unflinching to this end as a result of the operation?

The discussion after all hinges upon the word "unflinching," and this term has been applied to processes which are beyond the possibility of direct observation. If we grant that a disturbance of growth equilibrium was what led to the reparative processes, and that equilibrium was in the end restored, it does not seem difficult to admit that each minutest step in the direction of restoring this equilibrium was selected from a medley of random reactions. Indeed, Holmes suggests that

cells which develop in the direction of the missing part receive those advantages which the symbiotic relation afforded the cells whose place they take. Differentiation in any other direction deprives them of these advantages and subjects them to other unfavorable conditions.

Nor need it be assumed that these responses are wholly random. Although it is incredible that each type of possible injury has been provided for in advance by a specific mechanism, it seems more than possible that certain reactions have been acquired which are of service in *any* emergency—a sort of "first aid to the injured," as we might say. After these preliminary steps of a general character—which are, as a matter of fact, the common precursors of regeneration¹⁸—the more special processes may be supposed to proceed in a tentative fashion.

All that is meant by "growth equilibrium," in this discussion, is such a normal state of metabolic balance that the growth of each part is checked through its organic relations with the rest. Attainment of this goal would bring the organism into a condition of "no stimulation," like that of the protozoan which has escaped from an unfavorable environment.

Since we commonly are able to observe only the final outcome of such a process, and overlook the minute steps

¹⁸ These steps are frequently retrogressive ones and include the loss of specialized structures.

by which it comes to pass, we are wont to believe that the reparative activities move directly toward the end which we observe to be ultimately attained. Thus Driesch tells us that

the process of restitution, perfect the very first time it occurs, . . . is the classical instance against this new sort of contingency. . . . Here we see with our own eyes that the organism can do more than simply perpetuate variations which have occurred at random.

What we see with our own eyes, as I have already said, is only a series of visible stages in the process of restitution. We *do not see* the inmost morphogenetic processes, physical and chemical, by which this end is attained.

Perhaps it may seem that the foregoing explanation merely resorts to the familiar expedient of throwing our difficulties back into an invisible realm where they are safely beyond the reach of scientific investigation. I would say first of all that even this type of explanation, which at least speaks in the language of known facts, is preferable to one which frankly abandons scientific principles altogether. And secondly, I would point out once more the possibility that this hypothesis is one which may in reality be put to experimental test. For any indication of a profiting by "experience," *i. e.*, of a shortening of the time required to effect a given regulative response, would harmonize well with the hypothesis that the response was at first effected through tentative steps. Indeed, such evidence, even now, is not wholly lacking.

It may be well to remind ourselves at this point that the perfect regeneration of missing parts, or the complete reconstruction of a mutilated embryo is after all an exceptional phenomenon. Many animals almost entirely lack the power of regeneration, while most injured eggs either die or give rise to abnormal embryos. These facts harmonize best with the view that regenerative processes are causally produced in the same sense as inorganic phenomena, and that they are not determined, in any direct way, by needs or ends to be realized. The forma-

tion of misplaced, supernumerary and other useless structures, and the occurrence of anaphylaxis, instead of immunization, certainly do not argue for the existence of a "primary teleology" in nature, though, of course, they do not wholly refute it.

On the other hand, the occurrence of these non-adaptive responses to growth stimuli is no more inconsistent with an intra-selection hypothesis, such as that here advocated, than is the occurrence of multitudes of non-adaptive structures or colors in nature inconsistent with the theory of natural selection. There must be rigid limitations to the operation of both processes. The task which I have undertaken here is not to explain structures and function in general, but the more modest one of trying to explain why certain among these are directed toward the conservation of the individual or the species. If various other vital phenomena are found to be non-adaptive, our difficulties ought not to be increased.

There are cases, it is true, in which some simple physical factor, such as gravity, or the plane of section, may determine whether the actual missing part is restored or a misplaced organ is the result. It certainly seems arbitrary to offer fundamentally different explanations in the two cases. Now, I have nowhere made the contention that the processes involved in regeneration are wholly random, in the sense of being unrelated to one another and to the past history of the individual. In normal development the processes are doubtless so concatenated that growth and differentiation proceed in a direct way with little or no "lost motion." And every detached portion of such an organism must receive its share of this established developmental machinery. The tendency to reconstruct the whole, to attain the normal specific form, is therefore opposed by another set of tendencies, urging it to develop as if it were still part of the undivided organism. As is well known, the outcome of this conflict of forces varies, depending upon the species of animal and the time of operation. We may have

either total or fractional development as a result. It does not seem unlikely, therefore, that in every case of regeneration the control of the "organism as a whole" is opposed, more or less successfully, by the specific growth tendencies of the various cells and tissues from which restitution proceeds. These might, in consequence, bring about the "autonomous" production of a wholly misplaced part.¹⁹ Thus the phenomena of "heteromorphosis" should seem to offer no insuperable obstacle to the views herein set forth.

Applied to the ordinary phenomena of regeneration, say to the restoration of an amputated limb, or even the lens of an eye, this hypothesis of achievement through experimentation would seem to make no impossible demands upon our imagination. We need only suppose that the absence of the missing part serves as a stimulus to varied and undirected metabolic activities, that such of these as serve to restore the normal condition tend to be continued and that growth equilibrium (absence of stimulus to growth) is not normally attained until the missing part is restored. The case would seem to be not very different from that of an animal finding its way out of an unfavorable environment. In both instances we may suppose the organism to be in a condition of "unrest" until the end is achieved. This condition may or may not be conceived in psychical terms. If so conceived, the notion would be philosophically legitimate, though scientifically unnecessary.²⁰

When, however, we consider Driesch's crucial case of the development of an entire organism from an embryonic fragment, the matter is admittedly far less conceivable. For this fragment has retained nearly or quite the same potentialities as the entire egg or embryo, in that its career of multiplication and growth is brought

¹⁹ This explanation of heteromorphosis is, I think, quite in harmony with that offered by Holmes (*op. cit.*, pp. 302-303).

²⁰ Cf. Baldwin's statement ("Mental Development," p. 177): "the life-history of organisms involves from the start the presence of the organic analogue of the hedonic consciousness."

to a close only through the attainment of the form which is typical for the species in question. Why should this ultimate condition of equilibrium be the same whether we start from an isolated blastomere, an irregular fragment of a blastula or a normal egg? Does it not seem as if the only constant feature in this case were the end itself? In considering the behavior of a protozoan, the stimuli may vary and the method of escape may vary, but the organism itself is the same. The "equi-finality" of the result—to use an expression of Driesch's—may be attributed to this fact that we are dealing with the same physico-chemical system, and one of the self-regulating type. But what of our various embryonic fragments? Are they not obviously different physico-chemical systems?

Now, after all, the difference between this case and that of a regenerating limb or lens appears to me to be only one of degree. The distinctions relate (1) to the stage in development at which the injury is inflicted, and (2) to the proportional part of the organism which is left to reconstruct the remainder.

1. As regards the first point, we must suppose that at each stage of ontogeny such a state of physiological balance is normally maintained as is appropriate to that particular stage. That the multiplication and differentiation of certain cells is profoundly influenced by the presence or absence of other cells is one of the assured results of experimental embryology. One need only cite the difference between the development undergone by an amphibian blastomere which is totally detached at the two-celled stage, and that of the blastomere whose partner has been injured by a needle-prick and left in position.

Thus we have as much right to assume for the blastula as for the adult animal that any disturbance of metabolic balance will be followed by varied responses, some of which will tend to restore the balance normal to that period. The fact that these responses are known to differ radically, following the same type of operation,

and that the result is often a very imperfect reconstruction of the whole, lends support to the view that the cells of the injured embryo "feel their way"—so to speak—back into a condition of mutual equilibrium. In some cases this equilibrium appears to be of a simple physical sort, as for instance, that which is brought about by the folding together of the edges of a blastula fragment so as to reconstruct the spherical form. But in most cases the factors are doubtless vastly more complex.

Once the reconstruction of the normal embryonic form is attained, the difficulties in understanding the further stages of ontogeny are no greater than we meet with in the case of an uninjured embryo—that is, unless we are encumbered by a preformation theory of development.

2. As regards the second point above raised, there is theoretically no greater difficulty in understanding how one tenth of an organism may restore the remaining nine tenths than in understanding how the nine tenths may restore the one tenth. As a matter of fact, in dealing with certain organisms, the size or shape of the piece, or the region of the body from which it is taken count for little in the outcome. But they do count for something, and that something is significant. It has been found in some cases, for example, that there are lower limits to the size of the pieces which may carry out development or regeneration. And in other cases, the position of the plane of section may determine whether a useful structure is formed or one which is wholly useless.

But whether or not the size or shape of the fragment count for anything in the reparation of a given organism, we find that the *species* from which it is taken counts for everything. There must, therefore, be something that is common to all detached portions of an organism which are capable of reconstructing the same whole. The portion in question may be an asexual spore or a fertilized egg, or it may be an isolated blastomere or other artificially detached fragment of either an embryo or adult organism. What is this greatest common divisor? Is it a unit of structure or is it a chemical substance?

There would seem to be no third possibility, as long as we keep within the bounds of scientific explanation. But a unit of structure may none the less be itself a chemical individual. Modern speculative physics refers all qualitative differences in the last resort to differences of structure, even in the case of the elements. And it has been suggested that the various specific protoplasms, which are responsible for the slightly different metabolic products of different species, owe their differences to stereoisomers, *i. e.*, substances which agree quantitatively in their composition, but whose enormously complex molecules differ as the result of some slight transposition of atoms or radicals.²¹

To the majority of present-day geneticists there is doubtless a ready answer to the question: what is this something that is common to all detached portions of an organism which are capable of reconstructing the same whole? It is likely that to most of them a completely satisfactory answer would be: *the cell nucleus*. Thus Jennings,^{21a} in discussing specifically certain of the questions raised by Driesch, assures us that "the recent study of genetics has shown that this [the chromosomal] apparatus is the system on which the peculiarities of development mainly depend. This system is not equipotential; the fate of its parts is not a function of their position; it has a complex structure with a corresponding complexity of action; altering any of its parts alters correspondingly the action of the system; irregular removal or disarrangement of the parts destroys the action."

Whether or not this aggregate chromatin matter of the nucleus constitutes the *minimum divisible* of the organism, as recent students of heredity are disposed to believe, is still quite undecided. For protozoa we are definitely able to state that this is not true. Experiments in regen-

²¹ Reichert, *Science*, November 6, 1914. This article contains much interesting evidence for the chemical distinctness of genera and species, and even of individual organisms.

^{21a} *Philosophical Review*, Nov., 1918, p. 586.

eration show that there must be smaller bodies within the nucleus, each containing the potentialities of the entire organism. Ritter^{21b} has recently insisted that the concept of *heredity* must be applied unreservedly to these one-celled organisms, many of which are quite complex in structure and undergo a true ontogeny. Indeed, the experimental studies of Jennings and his students have demonstrated the transmission of individual peculiarities, both of structure and function. As for the metazoa, despite the considerable evidence for chromosomal "individuality" and for the localization of genetic "factors," it seems to be entirely premature for us to assume the existence of a mosaic of parts, rigidly predetermined and incapable of making good a loss. One should recall what happened to an earlier "mosaic theory" of development.

To go to the other extreme, it might be supposed that for each form of organism there was at least one substance, or molecular structure, which was typical for it, and which determined its specific physical and chemical characteristics. The other constituents of the adult body would be modifications of this typical substance, which had lost certain of its original components or acquired new ones. This specific protoplasm would have some points in common with the "germ plasm" of Weismann. It might be credited with the power of indefinite growth and self-division, so long as these were not checked by counterbalancing forces. When completely checked, a growth equilibrium would be established which would represent the normal form of the species in question.

The rather vague and indefinite point of view here suggested would avoid, however, the tangle of unverified assumptions that are involved in the hypothesis of a "germ-plasm," conceived as an aggregation either of Weismannian "determinants" or twentieth-century "genes." The admitted possibility that certain material particles of the nucleus are functionally related to separately heritable adult characters does not constitute

^{21b} The Unity of the Organism, Chapt. XII, XIII.

a proof that the entire organism develops through the combined activities of such particles. Moreover, even if such a complete germinal representation of adult characters were shown to exist, only a part—and a minor part—of our difficulties would be solved. We should still have to explain how the elementary parts of the body came to arrange themselves in proper spatial order and in proper chronological sequence during development. Blocks do not build themselves into houses. Driesch points out that historically vitalism and epigenesis have always been closely related, while the mechanistic school has commonly adopted some form of preformationism. Such a connection is far from being logically necessary, however. To me it would seem that preformation lent itself most readily to vitalism—to the notion of a builder who put the blocks together. In our particulate theories of organic differentiation, we commonly leave out of account the spatial and chronological relationships of the parts, or rather we take them for granted. We assume that somehow our “organismules” will find their way to their proper places at the proper moments, just as in a laboratory experiment the experimenter himself sees to it that everything is at each moment just where it belongs.

Let us return to an illustrative case, already considered, and ask why no one has ever seriously proposed a preformation theory of the earth's origin. Most moderns (M. Bergson is an exception) believe that our present world was the inevitable outcome of forces that were inherent in a fairly homogeneous molten mass, interacting with those of its cosmic environment. It has never been thought necessary to invoke the aid of special “determinants” to account for the various geographic and geologic features of our planet's structure. In dealing with inorganic things we are content to let our analysis rest, in the lack of more detailed information, with the acceptance of such general principles as “creative synthesis” or the “multiplication of effects.” We simply

have to admit that differentiation means just this fact of *de novo* formation. Otherwise it means nothing at all.

We must, however, recognize certain essential differences between the development of a sea-urchin from an egg and that of our world from the structureless spore which was long ago liberated by its nebular parent. Let us suppose that some experimental cosmogonist, using the refined technique of a Morgan, Roux or Driesch, had skilfully removed about three quarters of our newly formed globe, leaving the remainder to reconstruct itself as best it could. The spherical shape would doubtless have been quickly restored, but is it likely that there would have formed in the ensuing ages just that same arrangement of Europe, Asia, Africa, America and the Islands of the Sea that we now find upon our maps? Unfortunately it is too late to perform this experiment, but I think that most geologists would expect a much modified world as the result. Indeed, if the excision had been made after the mixture of molten substances had begun to separate we should be perfectly certain that a quite "abnormal" world would have been the outcome. All this may be granted.

Let us ask another question. Why is it that no modern thinker²² has set forth a preformation theory of *racial* evolution? It is only in accounting for individual development that this has been thought necessary. Yet the same paradox of *de novo* formation would seem to confront us in both cases, while other essential points of resemblance between phylogeny and ontogeny have often been pointed out.

One difference, doubtless, is that every process of phylogeny is regarded as a unique thing, while ontogeny is merely the *n*th reduplication of a known type, the character of which can be stated in advance. Hence it is that we are satisfied to resign the former process to the realm of "chance," while the latter we come to look on as determined in advance. Another difference seems to be that we look upon racial evolution as largely swayed by exter-

²² We must except Bateson.

nal factors, of the haphazard sort which operate in the realms of geography and meteorology; while individual development appears to be swayed chiefly by internal factors, and to pursue its preordained course in a high degree independent of the outside world.

But where in all this is the necessity for preformation? That two specific types of protoplasm, under identical conditions of environment, will give rise to widely different organisms implies, of course, considerable difference in the protoplasms. It does not, however, compel us to believe in the existence of correspondingly numerous differences in the two cases. A single initial difference between two physico-chemical systems may determine a multitude of differences at the end. For example, the presence or absence of a certain amount of annual rainfall on a given area of the earth's surface would determine the nature of an indefinite number of other characteristics, both geographical and biological. We do not in this case endeavor to pick out a particular element of the cause to account for each particular element in the effect. Driesch's assumption that any "mechanical" (*i. e.*, non-vitalistic) conception of the developing organism must be based on a preformation of parts may once more be dismissed as untenable.

Some preformation there is to be sure. Recent Mendelian studies, particularly the investigations of sex determination, make it highly probable that certain adult characters, though perhaps in no case single anatomical structures, are represented by spatially separated particles in the nucleus. Furthermore, a certain amount of "promorphology" has been demonstrated in the cytoplasm of the unfertilized egg, though this is perhaps to be regarded as representing merely an early stage in individual development. I feel bound to express the belief, however, that many recent students of Mendelian inheritance have carried their factorial speculations far beyond the evidence, and that their detailed localization of representative particles may prove in the future to have more interest for psychology than for genetics. We

are dealing with a field in which ever more minute differences are being distinguished—many of them by purely subjective tests—and one in which the ratio of inference to observed fact is ever lengthening. May it not be that we have here hitherto unsuspected possibilities of self-deception on the part of even our most competent investigators? The subject is one which seems to me to deserve more attention than it has received.

On the whole, we are not compelled to assume the existence of any more preformation than can be experimentally demonstrated. And it may be regarded as settled that we have no parcelling out of “determinants” to appropriate cells during ontogeny, such as Weismann imagined. The “sex chromosomes,” which seem to be the best authenticated instances of material bearers of hereditary traits, do not pass into definite body cells in the course of development and thus give rise to the primary and secondary organs of sex. Rather are they to be found distributed in every cell of the body. The assumption that they set free their characteristic determinants only in particular cells has no experimental or observational foundation.

Now, I am quite aware that any such “intra-selection” hypothesis of organic regulation as has here been advocated will be rejected by a large proportion of biologists on the ground that it is entirely superfluous. Various types of self-regulating mechanisms have been found in the non-living world, and the phenomena of growth and regeneration have long been known to be duplicated in crystals. Przibram has gone to considerable lengths in pointing out analogies between the behavior of the so-called “fluid crystals” and that of a regenerating organism.²³ And these analogies are reinforced by further ones, based upon the regeneration of crystals of hemoglobin. Many characteristically “vital” phenomena were

²³ (*Archiv für Entwicklungsmechanik*, October 16, 1906.) Likewise Torrey (*Scientific Monthly*, December, 1915) has discussed some interesting analogies between certain inorganic phenomena and the processes of “acclimatization” and “regulation.”

observed by him in these studies, among which the most impressive was doubtless the making over of a softened hemoglobin crystal by a process of "morphallaxis," *i. e.*, the readjustment of the matter already contained in the fragment. There must thus be recognized in these non-living masses of matter a tendency toward the attainment of a specific form. And it seems plain that this tendency may realize itself in more than one way. Yet we should never, in this case, think of proposing any hypothesis of "trial and error," nor speak of the choice by the crystal of "means" to an "end."

Now, I will hasten to express my own belief that the phenomena in the two cases do not differ in any very fundamental way. *I am disposed to regard the regeneration of a crystal, the reconstruction of a mutilated organism, and the solving of a problem by a mathematician as members of a single series of increasing complexity. They have in common the reattainment of a condition of equilibrium which has been overthrown.* The fact that the organism is possessed of life, or that the mathematician has a conscious end in view do not alter the situation.

Such a "regulative" tendency in the inorganic world is recognized by physical chemists as the "principle of mobile equilibrium," or the "theorem of Le Chatelier." As stated by Lewis,^{23a} this law asserts that "when a factor determining the equilibrium of the system is altered, the system tends to change in such a way as to oppose and partially annul the alteration in the factor. The same idea is conveyed by saying that every system in equilibrium is conservative, or tends to remain unchanged." Bancroft^{23b} has given to this principle the dignity of a "universal law," pointing out analogies in the realms of biology, sociology and economics. More recently, its importance in ecology has been urged by Adams.^{32c}

^{23a} "A System of Physical Chemistry," Vol. II, 1916, pp. 140-141.

^{23b} *Science*, Feb. 3, 1911.

^{23c} AMERICAN NATURALIST, Oct.-Nov., 1918; Jan.-Feb., 1919.

In the regeneration of the more familiar type of crystal, the latter doubtless goes about its task "unhesitatingly," we may believe. But this is not true of every inorganic system. "In a stream [of water]," says Jennings, "opposing actions of all sorts are combatted in ways almost as varied as in organisms: a hole is filled up, a dam overflowed, an obstacle circumvented, another obstacle floated away, a bank of earth undermined or cut through; and the stream finally reaches the sea."²⁴ Must we not recognize important points of resemblance between such behavior and that of a penned-up cat, scratching wildly at the objects in its cage until finally a way out is found?

But if we admit this essential unity between the living and the non-living in respect to their method of correcting a disturbed equilibrium, why should we have resort in one case more than the other to a theory of "contingency" as regards the relation of means to end? Why may we not suppose the regulative processes of protoplasm to proceed as directly toward a goal as those of a crystal?

Answering the first question, I would say that the conception of contingency has been introduced into this discussion merely in the sense of a denial of teleology. Such a denial has been deemed necessary only in the case of organic phenomena. For inorganic events are seldom thought of as governed by "ends," and the question of "means" does not therefore arise. But in this respect there is really no difference between the living and the non-living.

The reason why the regulative processes of protoplasm probably do not proceed as directly toward a goal as those of a crystal lies, I believe, in the vastly greater complexity of the former. But it does not seem likely that any rigid distinction can be drawn. If it is really true that a damaged crystal of hemoglobin can restore its original form without the taking on of new material, it seems hardly likely that this rearrangement is effected

²⁴ *Johns Hopkins University Circular*, 1914, No. 10, p. 16.

by the simple transfer of material from one point to another along the straightest possible paths. There is doubtless much random molecular movement which serves only to retard the consummation of the process.

*The more complex the system with which we are dealing, the more of these "fortuitous" steps will intervene between overthrow and recovery of equilibrium. The chances that an entirely new disturbing factor will directly call forth the means to its own removal will correspondingly decrease. The more plainly, therefore, will the adjustment proceed in an "experimental" fashion.*²⁵ Processes which favor the restoration of equilibrium (i. e., which satisfy the need) will be accelerated; those which work in a contrary direction will be retarded.

At this point it may be profitable to cite certain closely related utterances of Jennings:²⁶

The condition which results in . . . regulative action is the presence, in a system, of a constant force, or stream of energy having a uniform tendency or direction (or set of such forces), together with intermittent forces having varied tendencies; whenever this condition exists, regulative action appears. . . . When the constant stream of energy is restrained for some time from producing its usual effects, it overflows in various directions, depending on the distribution of the resistance and amount and intensity of the free energy. It thus produces one effect after another. Often, at the end, one of these effects is of such a nature as to overcome or avoid the restraint; the stream of energy may then continue in the channel thus opened.

Has our prolonged discussion now led us, after all, merely to a denial of the scientific validity of the adaptation concept? I think not. The concept of adaptation stands upon the same footing as those of life, organization, function, food, enemy, offspring, environment, stimulus, heredity and the scores of other indubitable facts with which biology deals. By the use of pedantic circumlocutions, all of these various expressions could doubtless be avoided, and our ideas thus squared with the most rigid demands of "mechanistic" philosophy.

²⁵ Of course, such expressions as "experiment" and "trial and error" must be used in a strictly objective sense, so far as they are given any explanatory value.

²⁶ *Johns Hopkins University Circular*, 1914, No. 10.

But would such a renunciation bring us any nearer to the truth? Only if we are ready to regard the whole science of biology as a provisional one, a mere temporary resting place on the way to the more "exact" knowledge which constitutes mathematical physics. How many of us are prepared to make this admission?

Before passing on to the next subdivision of our field, a few words are desirable in answer to another general criticism which may be raised against the line of argument here followed. Exception may be taken to the apparent assumption that the responses to a new situation, whether physiological or psychological, are wholly random. Many responses are so obviously direct and unvarying as to appear "fatally" determined.²⁷

Again, even where "experimentation" or "trial and error" is admittedly concerned in the process, the tentative efforts frequently lie within a quite restricted range of possible movements, and from the first approximate the goal to be reached much more nearly than if they were wholly undirected. Thus the experiments of Hobhouse²⁸ upon various mammals suggest to him "that recent writers have overestimated the effect of pure accident." Furthermore, he concludes that "the more a success was accidental the less likely were the animals to take advantage of it." So, too, in learning to throw at a mark, we do not commence by casting our missiles indifferently in every direction, but from the outset we throw them in the general direction of the target. And the same is palpably true when we attempt the solution of a mental problem. The trains of thought are doubtless "spontaneous," as pointed out above, but certain more or less relevant trains are favored in advance. It is from these that our selections are made.

Now, all these difficulties seem to me more apparent than real. After the first dawn of conscious experience, no situation is wholly new. Every problem which arises contains elements in common with earlier ones which we

²⁷ It is these which Loeb seems to regard as the more typical ones.

²⁸ "Mind in Evolution," 1915, pp. 236-237.

have already solved. This is the more true the more complex our problem. The "newness" of the latter may relate to a very few features, the residue consisting of elements which, in the last analysis, have been solved in an entirely empirical fashion. And the same may doubtless be said of those adaptive physiological responses which are generally assumed to be unconscious. As regards the fixed reactions known as "tropisms," I have already pointed out the probability that the predominantly adaptive character of these has been the outcome of racial history and therefore of some form of selection.

V. EVOLUTION AND "CONTINGENCY"

In the two preceding sections of this paper stress has been laid upon manifestations of the power of self-adaptation in the individual organism. Very little has been said regarding those fixed structural and functional mechanisms by which the more usual needs of life are provided for. The origin of such structures and functions—"adaptations," as they are familiarly called—must be accounted for in any adequate theory of evolution. Now, I have already argued that no theory of evolution, so far as it is scientific, can admit the possibility that the needs of the organism may call forth in any direct way the initiation of those processes by which these needs come to be satisfied. Let us look somewhat further into this question.

The field of organic evolution is one which has lent itself in a high degree to vitalistic and quasi-vitalistic exploitation. From the time of the establishment of the doctrine of descent, there were always persons who, in spirit, still clung to the creation principle, while accepting in form the newer ideas. Indeed, among biologists themselves, there have always been those who have seen in organic evolution the working out of a "perfecting principle," in a large degree independent of environment. Even Lamarck, who propounded one of the chief naturalistic accounts of this process, admitted that life

"tends by its very nature to a higher organization."²⁹ The botanist Naegeli is one of the best known exponents of such a view. With some, like St. George Mivart, the question has been closely interwoven with special theological beliefs.

This writer believed in an "innate tendency to deviate at certain times and under certain conditions," which tendency he held to be "an harmonious one, calculated to simultaneously adjust the various parts of the organism to their new relations." And this guiding hand seems to have been exercised not only in the direction of satisfying the needs of the organism itself, but in adapting the latter to the needs of man. Speaking of the evolution of the horse, he tells us:

The series is an admirable example of successive modification in one special direction along one beneficial line, and the teleologist must here be allowed to consider that one motive of this modification (among probably an indefinite number of motives inconceivable to us) was the relationship in which the horse was to stand to the human inhabitants of this planet.³⁰

Others, like Wallace, have had recourse to such a guiding principle only in accounting for the origin of man.

In recent years, the philosopher Bergson has adopted a vitalistic theory of evolution, weaving it into a metaphysical system of which an important feature is the essentially creative character of time or "duration." We see the world of living things moving grandly on through the ages, impelled by a mysterious force, the "*élan vital*," and flowering out spontaneously into a never-ending succession of living wonders. Such a conception may stir the imagination, but it does not add to our knowledge.

Now, curiously enough, this "teleological" factor has been introduced by various writers to explain two exactly opposite classes of cases: (1) the origin of adaptive char-

²⁹ *Philosophie Zoologique* (Elliot's translation), p. 239, and elsewhere. Lamarek's statements are not wholly consistent; however, and I cannot feel quite sure that he had in view any principle distinct from the one with which his name is commonly associated.

³⁰ "Genesis of Species," p. 151.

acters (Paley's argument), and (2) the origin of highly perfected structures and functions which are not believed to be adaptive in the biological sense, at least to the extent of influencing survival. The musical and artistic faculties of man belong to this second class.

Natural selection, as is well known, provides us with at least a formal explanation of the first class of characters, but not of the second. Lamarckism, with a varying degree of plausibility, accounts for the origin of characters belonging to either class. That both of these theories are, in last analysis, theories of selection has been pointed out in section II.

But the claim is to-day heard on various sides that both natural selection and Lamarckism have broken down completely, and that no other existing evolutionary theories merit serious attention. So impossible is it for some biologists to square the widespread appearance of adaptation in nature with their own special theories of life that they seek to escape the dilemma by declaring this appearance to be largely illusory. Thus Loeb³¹ tells us:

While it is possible for forms with moderate disharmonies to survive, those with gross disharmonies can not exist and we are not reminded of their possible existence. As a consequence the cases of apparent adaptation prevail in nature.

In much the same vein, Davenport³² writes:

Strictly, we may say adaptation is not the thing that is brought about, but rather absence of non-adaptedness. Such adjustment as we find is, doubtless, only such a residuum of variants as has not proved incompatible with conditions of existence.

One might profitably compare such conclusions as the foregoing with the findings of Cannon,³³ based upon the detailed study of certain adaptive mechanisms in man. To most of us the conviction is doubtless irresistible, not that such mechanisms now exist because of their *harmlessness*, but that they came into existence, step by step, *on account of their utility*.

³¹ "The Organism as a Whole," p. 344.

³² AMERICAN NATURALIST, August, 1916.

³³ "Bodily Changes in Pain, Hunger, Fear and Rage," 1916.

Taking heart from this skepticism among the biologists themselves, reactionaries are boldly coming forward with the assertion that the evolution principle has been discredited. It is certain that the spread of such ideas is not calculated to further the advancement of knowledge. Lack of an adequate hypothesis is not disproof of any possible hypothesis.

Moreover, it would now seem that some of these admissions of inadequacy have been premature. Much of the recent abandonment of the natural selection theory has been due to neo-Mendelian dogmatism. Selection, it is claimed, can only separate strains having different mean characters. It can not change the mean characters of a pure strain. But the experiments of Castle and some other breeders may be cited as evidence that such a contention is far from being established. And even those who reject Castle's interpretation of these results have been forced to concede that in some cases selection may bring about the indefinite modification of our stock—call the process "sorting" if we will.

So, too, the Lamarckian principle occupies the curious position of being dogmatically denied or wholly ignored by a large and influential class of writers, at the same time that others are able to adduce apparently convincing arguments for its reality. We certainly have a vast array of indirect or circumstantial evidence for this principle, derived from an inspection of the actual products of evolution as we find them. And we have a certain amount of direct, experimental evidence which can not be thrown aside as irrelevant or untrustworthy. While, therefore, sweeping conclusions regarding the Lamarckian factor are doubtless premature, the dogmatic denial of this factor very nearly amounts to self-stultification.

Thus, if we may read the signs of the times, the two chief naturalistic explanations of evolution may survive the fire of destructive criticism and again play an important part in our interpretation of life. By this, I do not wish to be understood as arguing that either or both of these theories constitute an adequate explanation (even

in the sense of a description) of how evolution has come to pass. For many years past, I have been endeavoring to weigh the evidence for and against both of these hypotheses and I have reached the same verdict with respect to the two: *each is both proved and disproved*. It is not that adequate evidence is lacking, as some assume. Rather, in each case, is the evidence well-nigh overwhelming—*on both sides*.

Now, obviously, no single proposition can be both true and untrue at the same time. What is meant here is this. I believe the selection of virtually continuous variations and the inheritance of functional and environmental modifications to have both played *some* part in evolution. And I do not hesitate to say that the evidence in favor of such a view is of the same general character as the evidence for the evolution theory itself, and nearly as convincing.

On the other hand, it seems no less probable that the operation of each of these factors is strictly limited. Indeed, it would appear likely that much of the adaptiveness in nature is not adequately accounted for by either process or by both taken together. There may well be other factors the existence of which is as little suspected to-day as was that of natural selection before the time of Darwin and Wallace.

But will our explanations remain purely naturalistic, or will they find room for extra-natural directive agents, by whatever name called? Will they, like the two chief historic theories, base themselves on the contingency of every adaptive variation in structure or function, antecedent to the test of experience, or will they be forced to concede a primary adaptiveness inherent in living matter.

Many of those who admit the widespread occurrence of natural selection as a process, are wont to deny to it any *explanatory* value. To quote a now familiar saying, it is said that the survival of the fittest does not account for the origin of fitness. The real cause of modification, these writers insist, is to be sought in the process by

which variations are produced and not in the fact that many of these variations fail to maintain themselves.

This argument is so plausible that it seems self-evident. And indeed in a sense it is. But there is another sense in which it is quite specious. Truly enough, no individual can survive which is not first born or hatched, or in some way brought into being by its parents. And those peculiarities which distinguish one individual from another are largely ushered into life along with it. They exist prior to selection. But fitness is a *relation*, not an absolute property of the organism. The word denotes merely a certain measure of adjustment to specific conditions of life, and the degree of this adjustment we know to vary almost indefinitely. To say that the conditions of life, acting through the selective process, can not be the cause of an increasing degree of fitness is like denying that a sculptor produces a statue, on the ground that he does not create the stone. It is well to note that even the sculptor's function is wholly selective. He eliminates certain portions of an unshaped mass of material.³⁴

The foregoing analogy admittedly fails in one important respect. It implies that the possibilities of selection in a given race are wholly unlimited. We know this to be very wide of the truth. The question to be answered here is merely whether or not they are completely *random* in the sense which has been employed throughout this article.

Now, some selectionists are wont to deny the completely random character of variation. So far as this is simply a denial of the infinite variability of any species, it is a mere truism. We may perhaps admit the possibility that a given strain might, through rigid selection, acquire the "habit" of varying preponderantly in certain definite directions, thus limiting the possibilities of further evolution within that group. And we might even grant that such definitely directed variations might ac-

³⁴ I do not recall the previous use of this analogy, but it is such an obvious one that it has doubtless occurred to many.

accumulate without the influence of selection at all (orthogenesis). But can we, without departing from naturalistic grounds, conceive of the production in this way of a structure in anticipation of a need? May we even conceive how appropriate variations could be called forth by an already existing need.

Of course, much obscurity of thought may be concealed beneath this innocent-looking word "need." What is a need? It is notorious that what is a luxury to some of us is a necessity to others. Our needs grow with our incomes. And this line of reasoning is directly applicable to sub-human realms. What an animal has, if this adjusts it to certain conditions of the environment, may be regarded retrospectively as the fulfilment of a need. Thus eyes fulfil the need of seeing. But can we say that such a need existed before the appearance of visual organs? There are beyond doubt still many forms of wave-motion or molecular vibration for which we have no organs of perception. Thus, in a large measure the organism creates its own needs, even in an unchanging environment. The word "need," like the word "end," is one which has a distinctly teleological implication. The more factors of the environmental complex an organism is brought into relation with, the better is it adjusted to its life conditions, and—other things equal—the higher position it holds in the scale of life. But these adjustments are only thought of as satisfying needs when we come to look back on what has actually happened.³⁵

There is a more limited sense, however, in which the use of this expression involves us in no such obscurities. All those fundamental requirements, such as food, oxygen, protection from enemies, etc., may be termed *needs*, without there resulting any confusion of thought. Now, anything which led to the removal of one or more of these fundamental requirements—say the drying up of a lake—might bring about the extermination of an entire species, unless some adaptive response were made.

³⁵ They may all, however, be properly termed *adaptations*, as has already been said.

Here, likewise, we may legitimately speak of the *need* for some sort of readjustment. Let us, then, restrict the word to anything without which a species would become extinct.

With this limitation of meaning understood, let us return to certain questions which I have left unanswered. Can we, on naturalistic grounds, conceive how an appropriate trend of variation could anticipate a given need; or can we even conceive how it could be called forth by an existing need? The former possibility certainly can not be admitted without frankly taking refuge in principles which lie beyond the range of scientific analysis. The latter possibility has, however, been vaguely implied by some writers on evolution.

So far as the "need" might be the result of some marked change in the environment or in the functional activities of the organism, it is credible that new variations might be offered to selection as a consequence of disturbances in the germinal material. But how could these occur preponderatingly in the direction of meeting the particular need in question? *Only in one way, so far as I can see, and that way is by the previous adaptive modification of the parent body.* For the latter may adapt itself experimentally, according to principles already discussed. The germ-cells could not adapt themselves experimentally, since the need is commonly one which does not as such affect them at all. Thus, the imperative demand for *directed* germinal variations—or at least ones of a useful sort—can be met, so far as now appears, only by assuming the transmission to the germ-cell of adaptive responses of the parent body.

The Lamarckian principle has the added advantage of being able to account for many of the "luxuries" of organization—adaptations, in the sense of fitting their possessors for a fuller and more varied life, but not of any conceivable survival value. Our own race, as has often been pointed out, is endowed with multitudes of such faculties. But we are sadly in need of direct experimental evidence along these lines.

Biologists of the future may recognize the importance of determining experimentally whether the germinal variations of a species ever respond to changed life conditions in such a way as to shift the mode of any character in the direction of greater adaptation. If such a general tendency as this were revealed, and if, at the same time, the transmission of somatic modifications were rigidly excluded, we should be brought to a crisis in the history of our science. The question at issue would not be merely the adequacy or this or that hypothesis. It would be the adequacy of our recognized scientific methods to deal with such problems. Despite the lengthy arguments with which I have sought to defend a purely naturalistic position, I should not, in advance, be supremely confident as to the outcome of such experiments. It might, after all, turn out that there was just such an "immanent teleology" in living things as the vitalists claim. If this should prove to be true, science would have to re-survey its territory and set itself new boundaries well within the old ones.

Such an undertaking, like that of settling once for all the "acquired characters" question, would doubtless be beset by great technical difficulties. But these difficulties should not be insuperable. So long, however, as "genetics" is held to be nearly or quite synonymous with Mendelism, evolution along dynamic lines is likely to languish. We must grant the enormous strides which have been made in our knowledge of the inheritance of certain types of variations, but the much more fundamental question of the causes of these variations is almost as far from solution as in the days of Darwin.

In conclusion, I would say a few further words in regard to my use of the expressions "contingency" and "chance" throughout these pages. It is needless to say that I have not used these words as synonymous with uncaused. I have spoken of an event as contingent, merely in the sense of its being causally unrelated to something else: for example, a variation in relation to a need to be fulfilled. Whether or not, in the last analysis, all things

are causally related in an Absolute, or whether the Universe is pluralistic in its nature, need not concern us here. That there may be some measure of pre-established harmony among its various parts is possible. It has recently been ably argued—and by a chemist, not a theologian—that there exists such a pre-established harmony between the organic and the inorganic worlds as a whole.³⁶

But even granting such very problematic relationships as this, we can not deny that much happens in a purely "accidental" way. No degree of fitness on the part of the environment for life in general can avail to prevent the wholesale destruction of organisms which "happen" into unfavorable surroundings. That all of the special adjustments between organism and environment arose primarily through contingency or chance in the sense here indicated is the main thesis which I have defended in these pages. There may be little of an original nature, either in the views proposed or the arguments used in support of them. But I believe that this essay may serve a useful purpose in bringing together a number of apparently distinct problems under a common viewpoint.

³⁶ L. J. Henderson: "The Fitness of the Environment" (1913), "The Order of Nature" (1917).

SHORTER ARTICLES AND DISCUSSION

PIEBALD RATS AND SELECTION, A CORRECTION

IN a recent important publication Dr. Sturtevant makes "an analysis of the effects of selection" in which he ably maintains the current view that the single gene is not changed by processes of systematic selection. His argument rests on a careful experimental study of the behavior of the character "dichaet" in *Drosophila*, followed by a general discussion of other work, my own in particular. I am represented as completely opposed to his view, and so I have been at times, but such is not the case at present. I agree so fully with his general conclusion that I want to obviate needless discussion based on the misapprehension.

I thought two years ago that I had evidence that a single gene had changed in the course of a selection experiment, this gene being concerned in producing the hooded pattern of rats. I now find this view rendered untenable by further experiments, the results of which are in course of publication. These results show that the supposed changes in a single gene are more probably due to changed residual heredity, which very likely may consist wholly of other "modifying" genes.

The crucial experiment was one suggested by Dr. Sewall Wright. The divergent hooded races, "plus" and "minus," resulting from selection, were to be crossed repeatedly with a third race, the hooded character being recovered as a recessive in F_2 following each cross and its variability compared with that of the uncrossed race. It was believed that if multiple modifying genes were involved, repeated crossing with a pure third race would tend to remove these, in which case the extracted hooded character being deprived of its plus modifiers would be substantially identical with the hooded character deprived of its minus modifiers, as seen respectively in hooded recessives derived from the plus and from the minus crosses. Well, they are substantially identical, but it has taken some time and a good deal of trouble to establish the fact. First we had to secure a satisfactory third race to use in the crosses, one free from contamination of any sort by crosses. This we sought in a wild race. But ordinary wild rats will not breed under laboratory condi-

tions. So we resorted to trapping immature wild rats from a single locality and using these as a foundation stock. Crosses with the plus race were then started successfully, but the corresponding experiment with the minus race was hard to get going and so has lagged behind the plus crosses. A report on the result of the plus crosses was made in 1916 (Castle and Wright). The crosses with the minus race were not then sufficiently advanced to show what their outcome would be and this was still true when reply was made to the criticism of MacDowell, as it had been previously when reply was made to Muller and to Pearl, and subsequently when I addressed the Washington Academy of Science on the rôle of selection in evolution (1917). But since then the minus crosses have given what seems to be conclusive evidence that the single gene had not been altered by selection, although the inherited complex responsible for the hooded character had steadily been altered in opposite directions and these alterations were permanent in the sense that they represented racial modes, stable so long as the race was not outcrossed.

I still have on hand a few representatives of the plus and of the minus races which because of their low fecundity it has been impossible to select further for several generations. The two races are very different in appearance. The plus race shows no white except on the under side and sometimes along the flank. The minus race shows no black except a short hood lying anterior to the shoulders, and in an occasional individual a small black spot or two in the middle of the back or on the tail. Yet the variability of each race is still considerable; as measured by our "grades" it has not appreciably diminished in recent generations. The somatic differences entailed by the selection experiments with the hooded character of rats are seemingly greater than those secured by Sturtevant or by MacDowell in regard to bristle number in *Drosophila*, yet I doubt not they may be explained on similar grounds.

Crossing with a wild race affects very differently the plus and the minus selected races. See Tables I and II. The plus race was much less affected than the minus race. Its mean grade was lowered, by three successive crosses with the wild race, not over three quarters of a grade. The standard deviation was about doubled by the first cross. That is the variability of the hooded character, when extracted in F_2 from the first wild cross, was

about twice as great as the variability of the hooded character in the uncrossed plus selected race. In the second and third crosses the variability declined somewhat, but was still considerably greater than that of the uncrossed race. It was indeed very similar to that of the plus race in the first seven generations of the plus selection experiment. (See Castle and Wright, p. 186.)

TABLE I

RESULTS OF REPEATEDLY CROSSING THE PLUS SELECTED RACE WITH A WILD RACE

	Mean Grade	Standard Deviation	Number of Hooded Young
Control, uncrossed plus race, generation 10	+ 3.73	.36	776
Once extracted hooded F_2 young	+ 3.17	.73	73
Twice extracted hooded F_2 young	+ 3.34	.50	256
Thrice extracted hooded F_2 young	+ 3.04	.64	19

TABLE II

RESULTS OF REPEATEDLY CROSSING THE MINUS SELECTED RACE WITH A WILD RACE

	Mean Grade	Standard Deviation	Number of Hooded Young
Control, uncrossed minus race, generation 16	- 2.63	.27	1,980
Once extracted hooded F_2 young	- .38	1.25	121
Twice extracted hooded F_2 young	+ 1.01	.92	49
Thrice extracted hooded F_2 young	+ 2.55	.66	104

The crosses of the minus race were started six generations later in the course of the selection experiments, with animals of generation 16, minus selection series. They show effects much more striking than those of the plus crosses. See Table II. The minus selected race had now attained a mean of -2.63. A single cross, with the same wild race used in the crosses of the plus series, lower the grade to -.38, extinguishing all the changes in mean grade made by sixteen generations of selection, and leaving the extracted hooded character in a highly variable state (standard deviation 1.25, nearly five times what it had been before). A second cross with the same wild race converted the extracted hooded individuals for the most part into a plus group, mean +1.01, but with variability somewhat decreased, standard deviation .92. A third cross with the wild race has given ex-

tracted hooded individuals *exclusively plus in character*, range from $+1.00$ to $+3.50$, mean $+2.55$. The variability has simultaneously fallen to .66, which is only about one third greater than that of the minus race in the first five generations of the selection experiment. (See Castle and Wright.) One family containing fourteen thrice extracted hooded individuals has a mean grade for the hooded individuals of $+3.05$, which is practically identical with the grade of the thrice extracted hooded individuals resulting from the plus crosses (Table I).

It thus appears that three or at most four crosses with a wild race suffice to obliterate all the racial differences which had been induced by ten generations of selection in the case of the plus race and sixteen generations in the case of the minus race. The plus race was changed almost immediately by a single cross, but the change was small (a fact which misled me until the results of the minus crosses were secured). The changes with the minus race were so great that they could not be fully secured by less than three or possibly four successive crosses (eight generations of offspring). The wild race, which we used in our crosses, evidently had a residual heredity much more like that of our plus-selected than like that of our minus-selected race. When the hooded gene from either race was introduced by repeated crosses into this residual heredity, the result was to produce hooded races of very similar grade, a little lower in grade than the plus selected race, but very much higher in grade than the minus selected race.

It thus becomes clear that the changes which had occurred in the hooded character as a result of selection were *detachable* changes and are probably in nature independently inherited modifying factors. This is a view which Phillips and I gave as one of two possible interpretations of the results which we published in 1914. Morgan, Muller, MacDowell and others have insisted that this was the only reasonable interpretation which could be given, but I have not been satisfied with this conclusion in advance of a really crucial experiment, such as I believe has now been performed. Meanwhile the probability that the theory of multiple modifying factors is correct as a general explanation of similar cases has been greatly strengthened by the work of Muller, Bridges, Sturtevant and others, showing that genetic factors, having a definite demonstrable position in linkage systems, influence in a particular way the somatic manifestation of char-

acters varying quantitatively or qualitatively. I accept their interpretations as correct in the light of our present knowledge.

I should feel like apologizing for my own obtuseness in not reaching a similar conclusion sooner, did I not recall with satisfaction how much clearer the rôle of selection now stands revealed than it did when these experiments were begun, and to the clearing up of the situation I shall at least hope that this rat work has contributed something, if only by provoking investigation.

The "Mutation Theory" of DeVries gave us a picture of selection as an agency temporarily effective in producing racial changes, but with those changes gradually vanishing as soon as the selection ceased. Johannsen denied within "pure lines" even temporary effectiveness of selection. A strictly logical use of Johannsen's conclusions would have limited their application to such organisms as he studied, self-fertilizing ones completely homozygous for all genetic factors and subject apparently to no new changes in such factors. But the doctrine was straight-way extended in the views of most geneticists to selection of every sort and he was treated as a traitor to Mendelism who saw any utility in selection or advocated its use as a means of improving the inherited characters of animals or plants.

The situation is wholly different to-day. Through the investigations of Jennings and his pupils on protozoa, of Stout on *Coleus*, and of Shammel on citrous fruits, the fact is clear that even within clones genetic changes may and do frequently occur and that systematic selection will serve to isolate these and thus lead to racial improvement. Those who have tried systematic selection in the case of cross fertilizing organisms have in some cases noted the occurrence of "mutations" with such frequency as to make progressive change under selection easily obtainable. Emerson and Hayes, in the case of certain pericarp color patterns of maize, find "mutations" so common that a wide range of variability results and selection is able to isolate, from such material, types "relatively stable," but very diverse in appearance. Modifying factors are not involved in Emerson's explanation of his results, but rather such instability of a single gene as leads to frequent mutation. Selection experiments with the variegated coat-patterns of mammals seem to involve less abrupt but otherwise similar changes, but modifying factors rather than repeated mutation seems to be the explanation required in view of the results of crosses reported in this paper.

That selection by one means or another is an effective agency in producing racial changes is not questioned to-day, as it was ten years ago.¹ The only question now at issue is whether the single gene is changeable. I am inclined to think, with Sturtevant, that while single genes do occasionally change producing multiple allelomorphs, a much more common occurrence is change in visible characters through modifying factors. Whether the direction of genetic variation is controllable, other than by the manipulation of modifying genes or the discovery of multiple allelomorphs remains to be determined. The evidence at present is largely negative. It is undeniable that liability to genetic variation is much greater in some organisms than others, much greater as regards some kinds of character than as regards others, but whether we can produce variability of a genetic character is quite a different question. We certainly at present have to follow nature's lead rather than to lead nature, as regards the course of evolutionary change.

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¹ Sturtevant's presentation of my views is a bit unfair in that it seems to imply that whenever I have spoken of "variation in a unit character," I have consistently meant variation in a single gene, whereas in discussing the case of the English rabbit, I have expressly reserved judgment on this point. In a large part of my experimental work, the question under investigation has been—do the visible characters which conform with Mendel's law in transmission suffer modification in crosses or as a result of selection? The present generation of geneticists has apparently forgotten that this was ever a debatable question. We all admit now that contamination occurs in crosses and that modification may be effected by selection, and we seek only to explain *how* the contamination is brought about (as by modifying factors) or *how* the modification is produced in the course of systematic selection (as by the isolation of modifiers in homozygous state). But in the days when the doctrine of gametic purity was under discussion, such "contamination" or "modification" was not admitted.

When Sturtevant denies the occurrence of "contamination," he uses the term in a very restricted sense, not as I have used it in the foregoing sentence, nor as it was formerly used in Mendelian discussions. What he means is not change in the visible character, as the hooded character of rats, but change in a single gene which is known absolutely to limit the manifestation of the hooded character in any form. I agree with his view that there is no conclusive evidence that this single gene had changed in the course of selection experiments, except in the case of our "mutant" race.

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